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Cover: *Bolboforma intermedia* Daniels and Spiegler (Incertae Sedis, possibly a calcified algal cyst) from Site 552A, southwest margin of Rockall Plateau, late Miocene NN9–10. × 800. *Bolboforma* was planktonic and cysts are found in epicontinental shelf sea deposits, thus providing a useful biostratigraphic link with oceanic sequences.

LATE TREMADOC GRAPTOLITES FROM WESTERN NEWFOUNDLAND

by S. HENRY WILLIAMS *and* ROBERT K. STEVENS

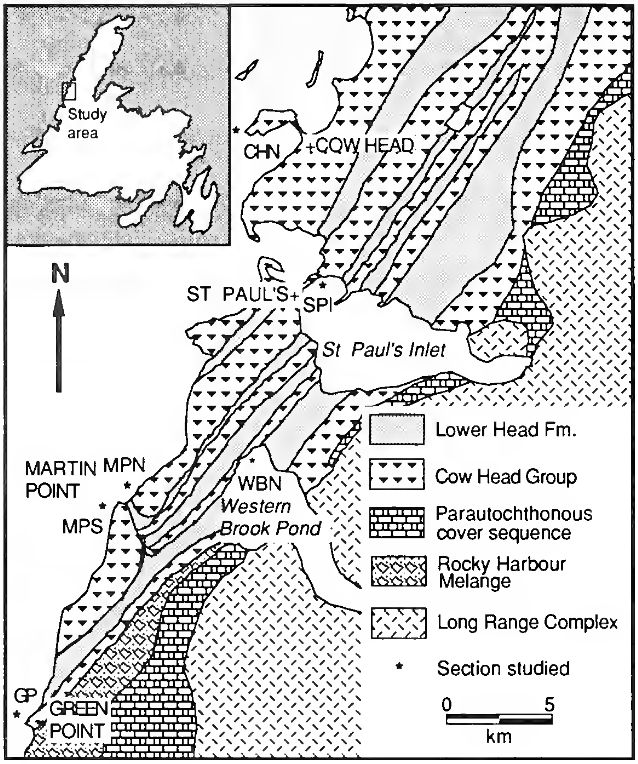
ABSTRACT. The Cow Head Group of western Newfoundland preserves a sequence of carbonate-rich sediments ranging from middle Cambrian to middle Ordovician. It yields a rich graptolite fauna both with flattened specimens in black shales and cherts, and three-dimensional and flattened material in nodular limestones which may be isolated from the rock by acid extraction. A continuous succession is present across the Tremadoc–Arenig boundary, containing a well represented graptolite assemblage which is here referred to the *A. victoriae* Zone. Late Tremadoc graptolite faunas have been documented from many localities around the world, but are commonly found in stratigraphically incomplete sequences and have only been known previously from non-isolated material. The Cow Head Group faunas comprise both flattened and isolated material, allowing detailed observation of proximal developments to be compared with overall rhabdosome forms. Several taxa possess overall forms, proximal structures and thecal styles somewhat similar to dichograptids and sigmagraptines found in the early Arenig, but they all possess a sicular bitheca; some have additional bithecae associated with the autothecae, and dichotomous branching is commonly far more variable. Because of these differences, all taxa described from this interval are considered to belong to the Anisograptidae, necessitating some generic reassignment and the erection of several new taxa. These include *Kiaerograptus undulatus* sp. nov. *K. magnus* sp. nov., *Paratemnograptus isolatus* sp. nov., *Aorograptus* gen. nov., *Adelograptus altus* sp. nov. and *A. filiformis* sp. nov.

DURING the latter part of the Tremadoc Series, some of the planktonic graptolites (traditionally assigned to the Dendroidea) which were components of Bulman's (1954) Anisograptid Fauna, underwent significant evolutionary changes. These involved the loss of bithecae and sclerotized stolons and general simplification of stipe geometry. This Anisograptid Fauna gave way to the typical graptoloid-dominated Dichograptid Fauna by the earliest Arenig. The adaptive reasons for the changes are not fully understood; the loss of bithecae which are generally considered to have played a role in reproduction (e.g. Kozlowski 1949; Rickards 1977) is particularly puzzling. Fortey and Cooper (1986) have challenged the traditional high-level classification of the graptolites; they assign all nematophorous (planktonic or epiplanktonic) graptolites to the Graptoloidea, including the anisograptids such as *Rhabdinopora* (ex *Dictyonema* – see Erdtmann 1982). In their scheme, only forms which remained benthic throughout astogeny are referred to the Dendroidea.

Cooper (1979*b*) reviewed the global distribution, zonation and correlation of Tremadoc graptolite assemblages. Late Tremadoc assemblages, which Cooper assigned to an Assemblage 4, are characterized by a large and diverse graptolite fauna including species formerly assigned to *Adelograptus*, *Bryograptus*, *Kiaerograptus*, *Temnograptus*, *Tetragraptus*, *Didymograptus* and *Clonograptus*. His following Assemblage 5 marks the base of the Arenig and is characterized by the appearance of *Tetragraptus approximatus*. Assemblage 4 faunas are perhaps best known from Australasia; other areas where they occur include China (southwest, Kiangsi), USSR (Kazakhstan, Taimyr), Europe (Oslo Region, Sweden and south-west Spain), and North America (Yukon, Texas, Quebec and western Newfoundland). Although many graptolitic units are therefore present through this interval, graptolites of late Tremadoc age are not commonly found well preserved, neither are they normally in sequence with stratigraphically older and younger, graptolite-bearing strata. In addition, evidence for a late Tremadoc age from other taxa is usually lacking, and little or no late Tremadoc isolated, three-dimensional material has been described to date.

Martin Point (Text-fig. 1) was the only locality in western Newfoundland discussed by Cooper

[Palaeontology, Vol. 34, Part 1, 1991, pp. 1–47, 7 pls.]



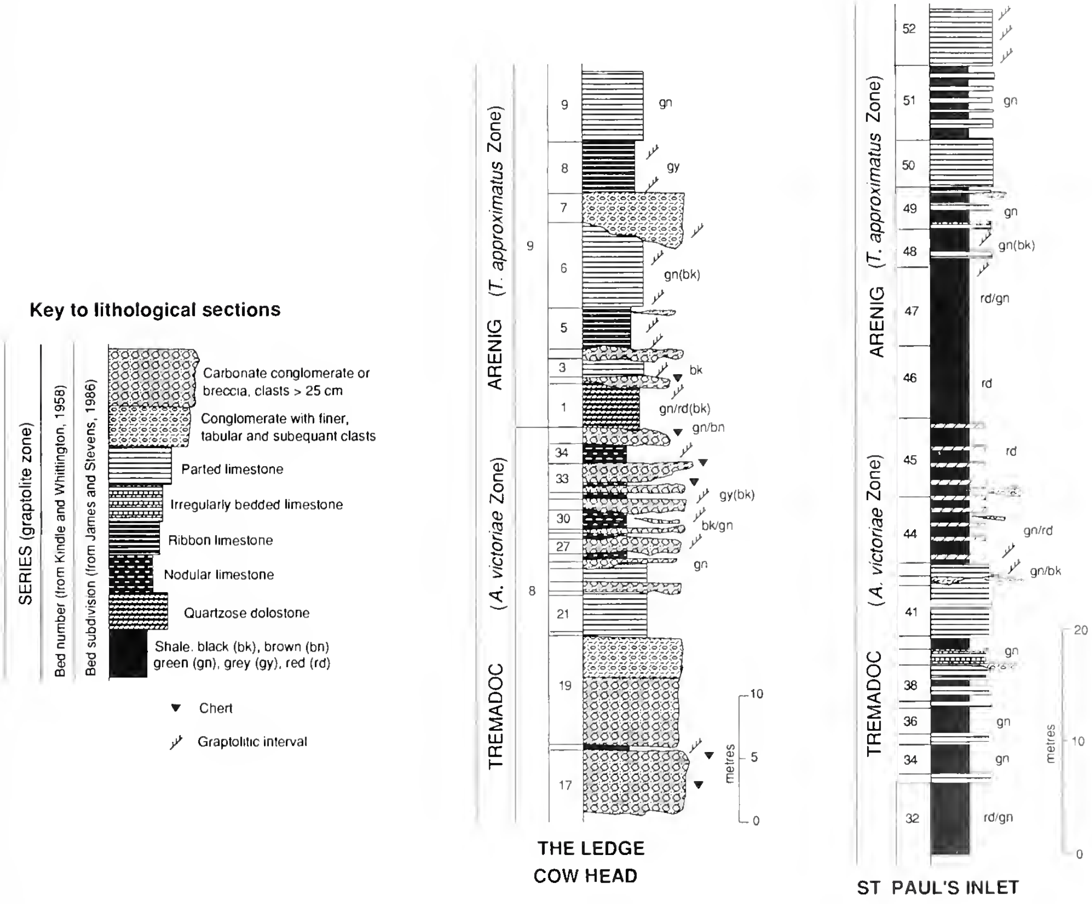
TEXT-FIG. 1. Geological map of the Cow Head region, western Newfoundland (after Williams and Stevens 1988, text-fig. 2).

(1979*b*). His data were derived from Erdtmann (1971*a*, *b*) who in turn had relied on preliminary information from Kindle and Whittington (1958). Since that time, other sections yielding late Tremadoc graptolites have been described by James and Stevens (1986), and it is both on Martin Point and these additional sections that the present paper is based. The importance of early Ordovician graptolites from the Cow Head Group has recently been illustrated through the work of Williams and Stevens (1988*a*), who described the Arenig faunas. Rich assemblages of flattened material are found in structurally-simple stratigraphic sequences, and are occasionally associated with three-dimensional, isolatable material from nodular limestones at the same horizons. Not only is there a stratigraphically-continuous sequence of graptolites from the late Tremadoc through to the earliest Arenig *T. approximatus* Zone, but the graptolites are also associated with other fossil groups within the black shales and nodular limestones, including conodonts and trilobites.

GEOLOGICAL AND STRUCTURAL SETTING OF THE COW HEAD GROUP

During the late Cambrian and early Ordovician, western Newfoundland formed part of the low latitude Laurentian continental margin, facing the Iapetus Ocean to the south-west (Williams and Stevens 1974). This area now lies within the Humber tectonostratigraphic zone of the Appalachians (Williams 1978). Two distinct sedimentary sequences were deposited along the margin; on the shelf itself, a predominately carbonate sequence (James *et al.* 1989) formed in shallow, tropic seas, while on the continental slope and rise a coeval sequence of shales and turbidites, the Humber Arm Supergroup, was deposited. The shelf/continental rise has since been destroyed by subsequent tectonism, and its former location can only be surmised (Rodgers 1968). That part of the Humber Arm Supergroup on the Northern Peninsula characterized by limestone conglomerates, thin bedded limestones, and shales is referred to as the Cow Head Group (Kindle and Whittington 1958; James and Stevens 1986).

The Humber Arm Supergroup, including the Cow Head Group, was transported westward during Llanvirn tectonism. It was pushed over the shelf sequence as part of a large allochthon, the Humber Arm Allochthon. Since the upper part of the allochthon contains large slabs of ophiolite-derived material and fragments of volcanic islands, the tectonism was probably the result of the abortive subduction of the Laurentian margin under Iapetus. Remarkably, the slices of allochthon containing the Cow Head Group escaped with little deformation during transport, although later (early Devonian?) imbrication resulted in some brittle-style deformation. The lack of pervasive alteration is demonstrated well by the conodont Colour Alteration Index (CAI), which reaches only 1·5 in the Cow Head region (Nowlan and Barnes 1987). As a result of these tectonic events and subsequent erosion, the Cow Head Group is now exposed in a series of thrust slices that span some 25 km across depositional strike (Text-fig. 2).



TEXT-FIG. 2. Lithological logs through the Cow Head Group for the Tremadoc–Arenig boundary interval at Cow Head and St Paul's Inlet, indicating graptolitic horizons (after James and Stevens, 1986).

Geology of the Cow Head Group

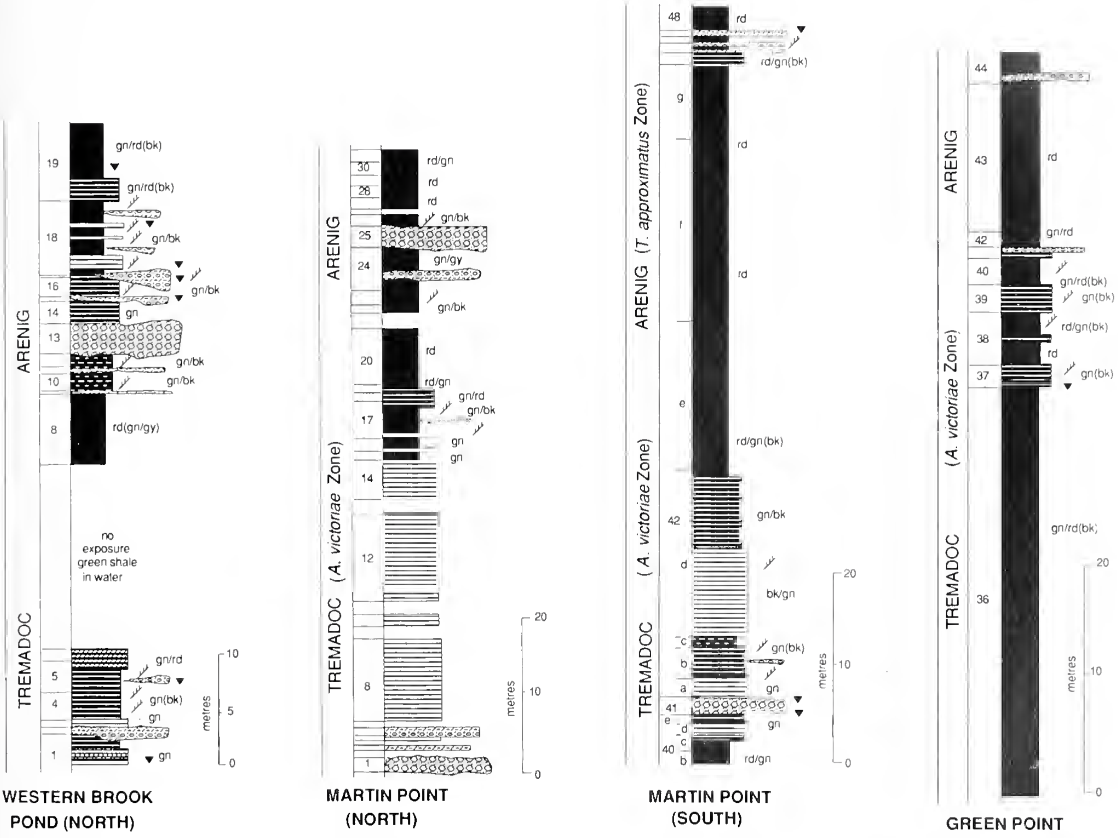
The following account is based largely on James and Stevens (1986), from whom additional details may be obtained. The Cow Head Group consists of up to 500 m of shales, hemipelagic limestones, carbonate grainstones and limestone conglomerates. The detrital carbonates were deposited through the action of lime turbidites and limestone debris flows derived in part from lithified or semi-lithified sediments of the shelf edge and upper slope to the north-west. Most, but not all, clasts from any particular conglomerate yield fossils from a limited stratigraphic range and are approximately coeval with fossils from the overlying shales and limestones. This permits an unusually high degree of correlation between typical shelf faunas and those inhabiting deeper, open ocean environments, although care needs to be exercised in recognizing reworked faunal assemblages. The most common fossils in the limestone clasts are trilobites (see Kindle and Whittington, 1958), brachiopods (see Ross and James 1987) and conodonts (see Pohler *et al.* 1987) of the North American conodont province. The interbedded shales and limestones yield graptolites, conodonts of the North Atlantic province, inarticulate brachiopods and occasional trilobites, together with rare examples of other invertebrates and possible fish remains. The graptolite record extends from the middle Cambrian to the early middle Ordovician (late Arenig); details of the post-Tremadoc, early Ordovician graptolites are given by Williams and Stevens (1987, 1988*a*). A fuller account of previous investigations into graptolites from the Cow Head Group is also provided in the latter work. Other recent publications on the invertebrate faunas include accounts of the conodonts straddling the Cambrian–Ordovician boundary (Barnes 1988) and the Tremadoc–Arenig boundary (Stouge and Bagnoli 1988), and notes on the Radiolaria (Iams and Stevens, 1988; Stevens and Iams 1988). A monographic study of the Cambrian trilobite fauna has recently been completed by Ludvigsen *et al.* (1989).

Biostratigraphic correlation between the isolated sections through the Cow Head Group, based mainly on graptolites and trilobites, shows that several conglomerate horizons can be traced throughout the entire Cow Head area. Those conglomerates in the most north-easterly exposures are thickest and coarsest, and interpreted to have been deposited closest to source. The most proximal sections of Stearing Island and Lower Head are composed almost entirely of conglomerate with only narrow interbeds; one boulder at Lower Head is 200 m across (Kindle and Whittington, 1958). The distal sections such as that at Green Point are mainly shale and thin-bedded limestone; here the conglomerates are thin with only small clasts up to 20 cm diameter.

The proximal sections in the Cow Head Group were originally upslope from the more distal, and this may have controlled the distribution of graptolites to some extent. A noticeable feature of the distal section is the development of red, bioturbated shales in the late Tremadoc and Arenig, although at Cow Head itself the only heavily oxidized sediments present are found in a 3·3 m thick greenish dolostone interval at the Tremadoc–Arenig boundary. The overall colour change in Arenig shale interbeds, from dominantly green and black proximally to almost entirely red in the more distal sections, suggests an oxygen minimum upslope, with increased ventilation in deeper waters as found at the present time (see James and Stevens 1986). The ubiquitous red strata across the Tremadoc–Arenig boundary must, however, reflect important changes in the structure of at least the western reaches of the Iapetus Ocean, and may be of global significance (Stevens in prep.). It is possible that a stratified Cambrian ocean with anoxic bottom waters changed into a mixed ocean with oxygenated bottom waters during the Tremadoc, perhaps as a result of the glacial event postulated by Fortey and Morris (1982). Such a change, particularly if it occurred during the Tremadoc–Arenig boundary interval, may well have influenced the course of graptolite evolution in a similar fashion to the extinction and radiation event during the late Ordovician (Barnes and Williams 1990).

Stratigraphic nomenclature of the Cow Head Group

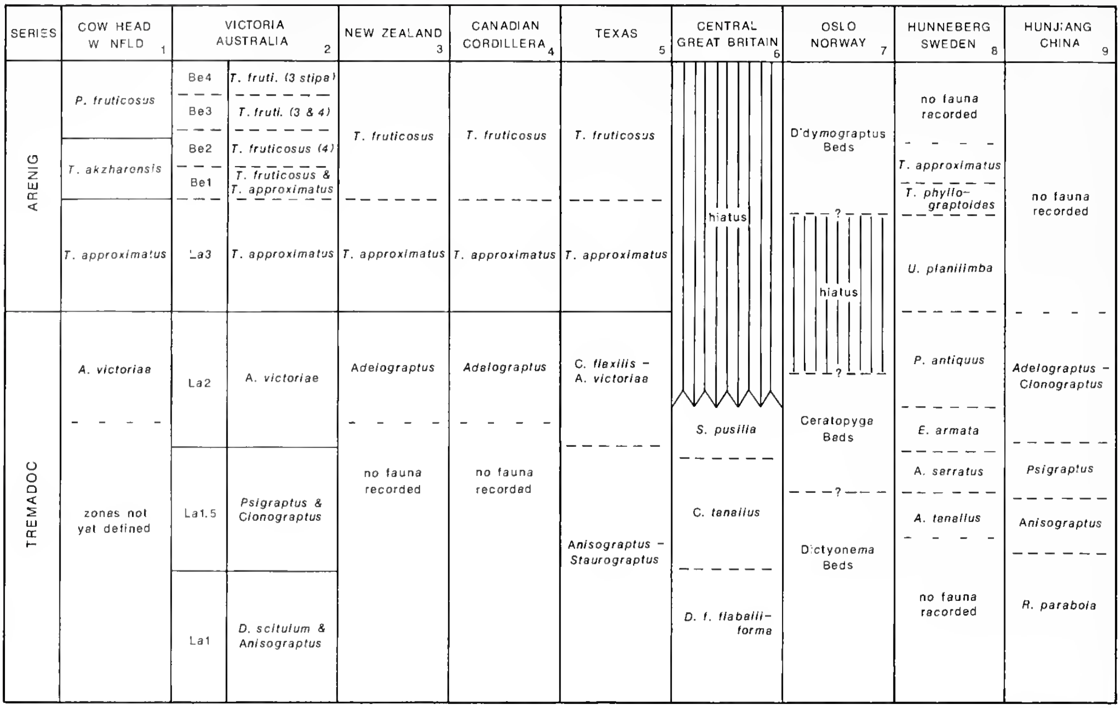
The earliest workers who studied the rocks of western Newfoundland, namely Richards, Billings and Logan (*in* Logan 1863), correlated the Cow Head strata with similar rocks in Quebec, particularly with those at Levis. Logan (1863) placed the Cow Head Group in his Division P. Schuchert and Dunbar (1934) concluded that the Cow Head was in part a tectonic breccia of middle Ordovician age. Kindle and Whittington (1958), following the lead given by Johnson (1941), recognized that the strata represented a sequence of sediments with an orderly stratigraphy and that the breccias were part of the package, rather than being later, tectonically-derived material. They used a sequence of numbered 'Beds' to describe the Cow Head section. These are not beds in the usual sedimentological sense, nor do they conform to formal lithostratigraphic convention as recognized internationally. Rather they are hybrid biostratigraphic/lithostratigraphic units defined on their fossil content and gross overall lithology. They are, however, convenient to use and were extended to all parts of the Cow Head Group by James and Stevens (1986). Strata yielding a late Tremadoc graptolite fauna occur in the upper part of Bed 8 (Text-figs 2 and 3), and are here assigned to the *Aorograptus victoriae* Zone. The base of this zone is as yet undefined, but the top is marked by the appearance of graptolites indicative of the early Arenig *T. approximatus* Zone at the base of Bed 9 (Williams and Stevens 1988*a*). The more formal lithostratigraphic nomenclature proposed by James and Stevens (1986) shows correlation with faunal changes at the Tremadoc–Arenig boundary only in the more proximal sections (e.g. James and Stevens 1986, fig. 43), where it lies at the boundary between the underlying Stearing Island Member and overlying Factory Cove Member of the Shallow Bay Formation.



TEXT-FIG. 3. Lithological logs through the Cow Head Group for the Tremadoc–Arenig boundary interval at Western Brook Pond, Martin Point and Green Point, indicating graptolitic horizons (after James and Stevens, 1986).

Correlation with other sequences

Full discussion of correlation between graptolitic zonal schemes of the early Ordovician was given by Cooper (1979*b*). Since that time, additional sections have been studied; we therefore include an



TEXT-FIG. 4. Correlation of the late Tremadoc–early Arenig graptolite zones of the Cow Head Group with other sequences (data based largely on: 1 – Williams and Stevens 1988*a* and this paper; 2 – VandenBerg 1981; 3 – Cooper 1979*a*; 4 – Lenz and Jackson 1986; 5 – Berry 1960; 6 – Stubblefield and Bulman 1929; 7 – Monsen 1925; 8 – Maletz and Erdtmann 1987; 9 – Wang and Erdtmann 1986).

updated correlation chart to include a selection of these (Text-fig. 4), although some (e.g. Hunneberg and Oslo) are currently under investigation and detailed biostratigraphic discussion is not yet possible. For the purpose of the present paper, we merely reiterate the precise correlation possible in continuously graptolitic successions across the Tremadoc–Arenig boundary interval, where a rapidly evolving graptoloid fauna, as found in the *A. victoriae* Zone in the Cow Head Group, becomes extinct and is then replaced by the somewhat low-diversity but distinctive dichograptid fauna of the *T. approximatus* Zone (see Williams and Stevens 1988*a*). Several anisograptid genera, including *Rhabdinopora*, surprisingly seem to have been unaffected by this evolutionary event, maintaining their relative abundance from the late Tremadoc through to the *T. akzharensis* Zone. These taxa are, however, rare in the succeeding *P. fruticosus* and later Arenig zones, where the fauna is dominated by dichograptids and sigmagraptines.

Justification for employing the chronostratigraphic series 'Tremadoc' and 'Arenig' is, however, more difficult owing to the incomplete nature of original British sections and the current state of flux regarding their definition (see Fortey 1988). Ongoing biostratigraphic studies within the Cow Head Group, particularly of the conodonts and trilobites (see Barnes *et al.* 1988; Stouge and Bagnoli 1988; Williams and Stevens 1988*b*), are permitting precise correlation between the various schemes at this level. These support the assumption made by most previous graptolite workers (e.g. Bulman 1970; Cooper 1979*b*) that the major faunal turnover documented at a level equivalent to the boundary between the *A. victoriae* and *T. approximatus* zones lie close to the traditionally accepted position of the Tremadoc–Arenig boundary.

TAXONOMIC PROBLEMS ASSOCIATED WITH LATE TREMADOC GRAPTOLITES

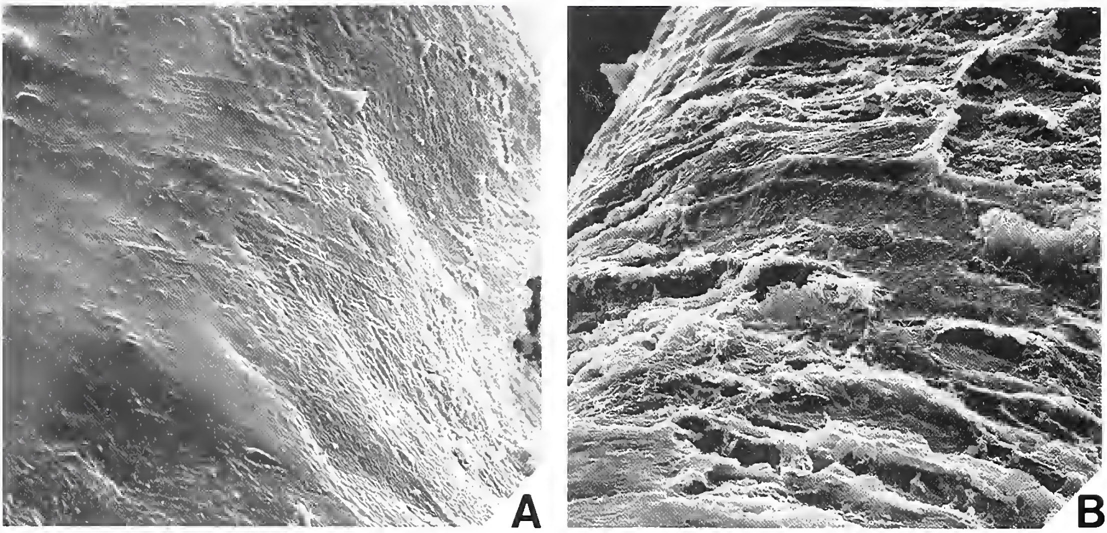
The earliest graptolites from the Cambrian were all benthic (see Rickards 1977); the first planktic graptolites evolved during the Cambrian–Ordovician boundary interval, including the ubiquitous and familiar group of *Rhabdinopora flabelliformis*. These Tremadoc anisograptids have traditionally been assigned to the Dendroidea, characterized by numerous, commonly irregular dichotomies, presence of bithecae, and a sclerotized stolon. Fortey and Cooper (1986) produced a revised high level, phylogenetic classification, in which they assigned all nematophorous (i.e. planktic and epiplanktic) graptolites to the Graptoloidea, restricting the Dendroidea to benthic genera. For the purpose of the present work, we accept this revised notion; consequently all taxa described herein are considered to be Graptoloidea.

Bulman (1970) referred all Tremadoc nematophorous graptolites to the Anisograptidea; these were subsequently split into four subfamilies, the Adelograptinae, Anisograptinae, Staurograptinae, and Rhabdinoporinae, although Fortey and Cooper (1986, p. 683) doubted that these groupings served any useful, phylogenetically-related purpose. Further studies utilizing isolated material such as the present one are required before any additional revision of high-level classification is possible; until that time we follow Fortey and Cooper (1986) in using an undivided family Anisograptidae.

Previous publications describing late Tremadoc graptolites have assigned them to both anisograptid and dichograptid taxa, for while some elements of the fauna (e.g. *Rhabdinopora*) are clearly identical to earlier Tremadoc taxa, others appear more similar in overall rhabdosome form to 'typically' Arenig dichograptids, commonly having only two to four stipes and relatively simple thecal style. These species have been variably assigned to anisograptid genera such as *Adelograptus* and *Kiaerograptus*, and to dichograptid genera including *Tetragraptus* and *Didymograptus* (e.g. Jackson 1974; Cooper and Stewart 1979). None of these previous studies had the opportunity of utilizing isolated, three-dimensional material to substantiate deductions made from flattened, non-isolated species. Most material described here from the Cow Head Group is flattened, but three nodular limestone horizons (at Martin Point South, Green Point and St Paul's Inlet) have yielded three-dimensional graptolites that can be isolated from the rock using acetic acid. These generally lack fine detail of periderm structure owing to the rather coarse, granular nature of preservation, probably related to partial breakdown of the organic material during subsequent burial and tectonic deformation. A few specimens do, however, reveal some ultrastructure, including cortical bandages overlying the fusellar increments (Text-fig. 5). Most studies of periderm ultrastructure have been made on graptolites of middle Ordovician and Silurian age, Rickards *et al.* (1982) recording no studies at all on material from the Tremadoc. Our material is thus important in providing a comparison of structures described from later taxa, although the main value of isolated specimens from the Cow Head Group is in permitting observation of proximal development. This has allowed us to make the following conclusions:

1. Whereas presence of bithecae associated with autothecae is variable, all taxa from this interval possess a sicular bitheca. A sicular bitheca has never been recorded from any Arenig dichograptid or sigmagraptine species, although it is apparently present in all earlier Tremadoc anisograptids (see Rickards 1975, 1977).
2. With the exception of the sicular bitheca, proximal development of several late Tremadoc species is almost indistinguishable from that of certain early Arenig dichograptid and sigmagraptine taxa described by Williams and Stevens (1988*a*).
3. Although overall rhabdosome form of a few taxa are similar to Arenig dichograptids and sigmagraptines, irregular occurrence of delayed dichotomies commonly results in extra stipes of variable number. This contrasts with the regular, fixed nature of branching in the Arenig taxa.
4. Genera such as *Rhabdinopora* and *Clonograptus* which are found earlier in the Tremadoc and continue through into the Arenig have distinctive proximal developments unlike those of the majority of the fauna, and bithecae throughout the rhabdosome.

We consider that the presence of a sicular bitheca and irregular dichotomous branching does not permit the assignment of any late Tremadoc graptolites to the Dichograptidae or Sigmagraptinae,



TEXT-FIG. 5. SEM micrographs showing details of ultrastructure on isolated metasicula of *Kiaerograptus bulmani* (Thomas, 1973), GSC 87446, SPI43 (complete specimen figured Pl. 3, fig. 12). A, cortical bandages, × 110. B, fusellar increments, × 110.

unless the traditionally accepted views of these high-level classifications is significantly modified. All taxa described herein are therefore assigned to existing or new anisograptid genera. It does, however, seem likely that several late Tremadoc genera give rise to Arenig forms through loss of bithecae and the fixing of dichotomous branching, perhaps suggesting a polyphyletic origin for the dichograptids and sigmagraptines. This will be the subject of a future study incorporating both Tremadoc and Arenig material, and is outside the scope of the present paper.

SYSTEMATIC PALAEONTOLOGY

Descriptive nomenclature employed conforms to that of Bulman (1970), Cooper and Fortey (1982) and Williams and Stevens (1988*a*). Particular note should be made of the term 'rutellum', introduced by Williams and Stevens (1988*a*, p. 20) to describe the 'lip' or 'spoon-shaped' process found at the sicular aperture of many Ordovician graptolites on the side of $\mathrm{th}1^1$ (*cf.* the virgella, which is a spine). The acetate overlay technique described by Williams and Stevens (1988*a*), p. 23) was employed to assist in distinguishing species and in comparing isolated specimens with flattened material.

Line drawings were made whilst using a Wild M5A microscope with 'camera lucida' attachment. Light photographs of isolated and non-isolated material were taken with a Wild M400 photomicroscope, using fibre-optic light source and with slabs immersed in 95% ethanol. Scanning electron micrographs were taken using a Hitachi S570 with a 120 film back.

All figured specimens are housed in the collections of the Geological Survey of Canada, Ottawa (GSC). Specimen localities and horizons in the systematic section are referred to in abbreviated form; collected sections (see Text-fig. 1 and Williams and Stevens 1988*a*) are the 'Ledge' on the Cow Head Peninsula (CHN), St Paul's Inlet, North Tickle (SPI), Western Brook Pond, north section (WBN), Martin Point, north and south sections (MPN and MPS), and Green Point (GP). Numbered intervals refer to those used in Text-figures 2 and 3.

Order GRAPTOLOIDEA
Family ANISOGRAPTIDAE Bulman, 1960
Genus KIAEROGRAPTUS Spjeldnaes, 1963

Type species. Didymograptus kiaeri Monsen, 1925, pp. 172–175, pl. 2, figs 9, 10, 12–14, 16, pl. 4, figs 6–8. By original designation.

Diagnosis (revised). Rhabdosome horizontal or declined, with two primary stipes, one or both of which may dichotomise at the second thecal pair to produce three or four stipes. Autothecae simple or with sigmoidal curvature, prothecal folds occasionally present. Sicula with bitheca; other bithecae present in early forms, apparently absent in later taxa.

Remarks. The definition of *Kiaerograptus* was revised by Bulman (1970) and by Cooper and Stewart (1979); the description of *K. quasimodo* by Rushton (1981) and of taxa in the present study necessitate a broadening of the understanding to include rhabdosomes with more than two stipes as originally defined.

Further revision might permit restriction of the genus to include only taxa with sigmoidally curved thecae and prothecal folds, as found in *K. kiaeri*, *K. quasimodo*, and the two new species erected in the present study (*K. undulatus* and *K. magnus*). This morphological feature is, however, often difficult to recognize in flattened material, and apparent folding of the dorsal margin is sometimes a post-mortem effect related to diagenetic flattening.

All species included within *Kiaerograptus* from western Newfoundland have similar proximal development, but show some variation in thecal style; none, however, possesses any bithecae other than that of the sicula, and possibly at the dichotomies of first order stipes. Species from earlier in the Tremadoc, such as *K. kiaeri* and *K. quasimodo* have bithecae associated with autothecae throughout much of the rhabdosome, and a gradual reduction in bithecae would probably be documented if a continuous stratigraphic succession of taxa could be found.

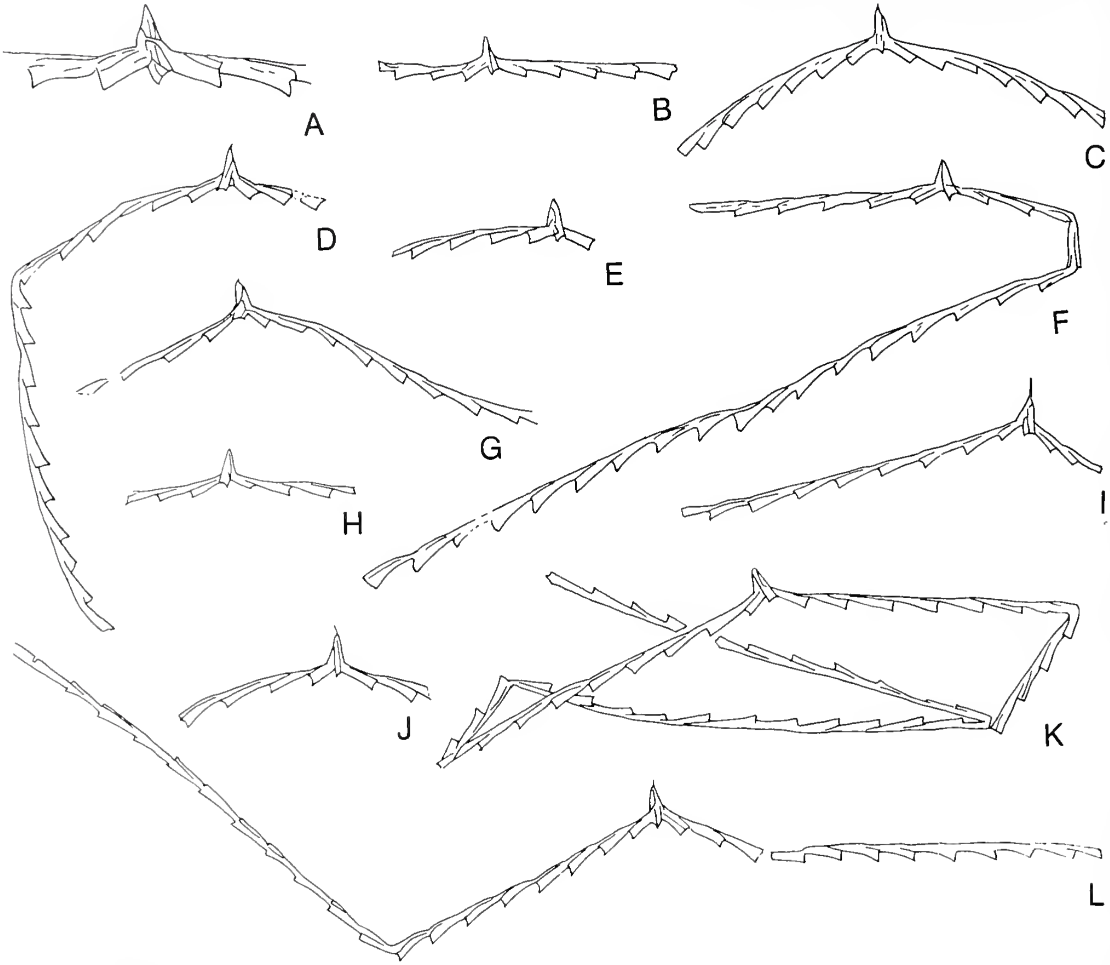
Kiaerograptus pritchardi (T. S. Hall, 1899)

Plate 1, fig. 1; Text-fig. 6A-L

1899 *Didymograptus pritchardi*, n. sp.; T. S. Hall, p. 167, pl. 17, figs 7 and 9; pl. 19, figs 8 and 10.
1938*b* *Didymograptus pritchardi* T. S. Hall; Harris and Thomas, pl. 1, fig. 13.
1960 *Didymograptus pritchardi* T. S. Hall; Thomas, pl. 1, fig. 14.
?1962 *Didymograptus tenuiramis* sp. nov.; Obut and Sobolevskaya, pp. 84–85, pl. 5, fig. 3.
1966 *Didymograptus pritchardi* T. S. Hall; Berry, pp. 429–430, pl. 45, fig. 1; pl. 46, fig. 1; pl. 47, figs 1 and 2.
1974 *Didymograptus*(?) *stelcki* n. sp.; Jackson, pp. 52–53, pl. 5, figs 5 and 7; text-fig. 1*a*, *b*.
non 1974 *Kiaerograptus pritchardi* (T. S. Hall); Jackson, p. 51, pl. 5, fig. 3; text-fig. 2*a*, *c*, *d* (= *A.*? *filiformis sp. nov.*).
1979*b* *Kiaerograptus* cf. *pritchardi* (T. S. Hall); Cooper, fig. 5*a*.
non 1982 *Kiaerograptus pritchardi* (T. S. Hall); Gutierrez-Marco, fig. 2*f* (= *K. taylori*).

Type specimen (designated Berry 1966, p. 429). The lectotype is Nat. Mus. Victoria No. P14238, figured by T. S. Hall (1899, pl. 17, fig. 7), from La2 near Lancefield, Victoria, Australia.

Diagnosis (revised, incorporating Berry's redescription of type material). Rhabdosome with two (or occasionally more) long, slender, gently declined stipes, straight or dorsally convex, widening rapidly from 0·4–0·6 mm proximally to a maximum of 0·5–0·9 mm. Sicula inclined, 1·0–1·5 mm long, 0·25–0·3 mm wide at aperture. Autothecae number 9–9·5 in 10 mm, overlapping two-fifths to one half of their total length, inclined at about 10° to dorsal margin. Bithecae apparently absent except for sicular bitheca.



TEXT-FIG. 6. *Kiaerograptus pritchardi* (T. S. Hall, 1899), GP38, all × 5 except A (= × 10). A and B, GSC 87381. C, GSC 87393. D, GSC 87390. E, GSC 87412. F, GSC 87383 (also figured Pl. 1, fig. 1). G, GSC 87368. H, GSC 87378. I, GSC 87411. J, GSC 87399. K, GSC 87406. L, GSC 87407.

EXPLANATION OF PLATE 1

Fig. 1. *Kiaerograptus pritchardi* (T. S. Hall, 1899). GSC 87383, GP38, × 10 (also figured Text-fig. 6F).

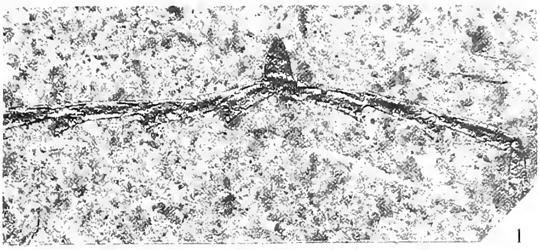
Figs 2–4. *Kiaerograptus undulatus* sp. nov. MPS42C, × 10. 2, GSC 87286. 3, GSC 87330 (also figured Text-fig. 8O). 4, GSC 87327.

Figs 5–7. *Kiaerograptus magnus* sp. nov. GP38, × 10. 5, GSC 87388. 6, GSC 87331. 7, GSC 87361 (also figured Text-fig. 8N).

Figs 8 and 9. *Kiaerograptus bulmani* (Thomas, 1963). MPS42C, × 5. 8, GSC 87329. 9, GSC 87317.

Figs 10–16. *Paratemnograptus isolatus* gen. et sp. nov. 10, GSC 87375, GP38, × 10. 11, GSC 87315, MPS42C, × 10. 12, GSC 87287, CHN8.30, × 5. 13, GSC 87384*b*, detail of distal branching, GP38, × 5. 14, GSC 87288, CHN8.30, × 2.5. 15, GSC 87385, GP38, × 2·5. 16, GSC 87289, CHN8.30, × 5.

PLATE 1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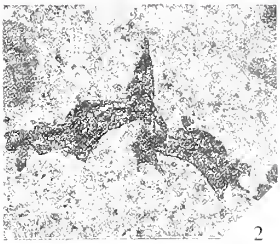
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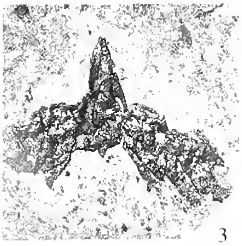
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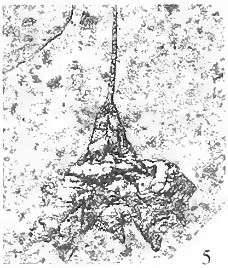
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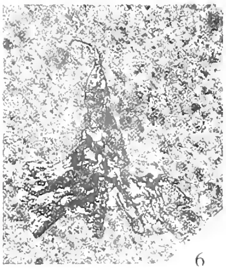
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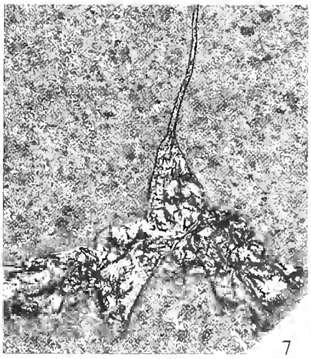
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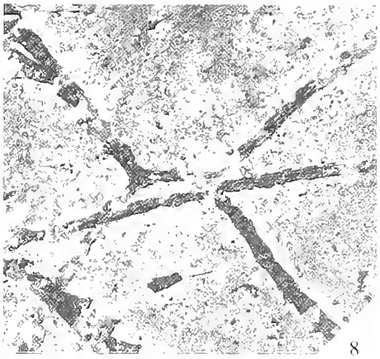
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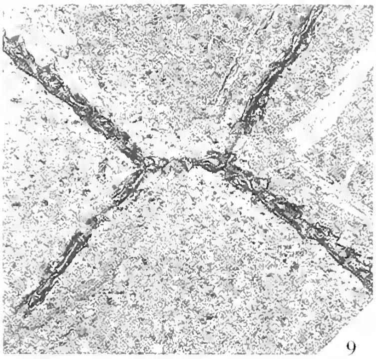
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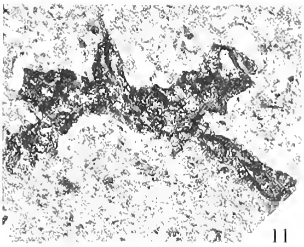
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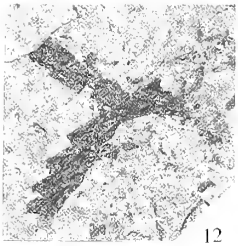
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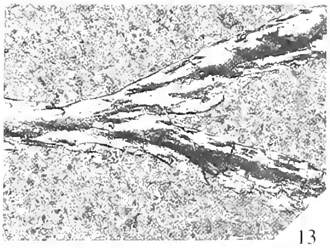
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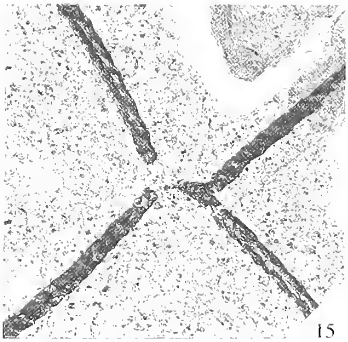
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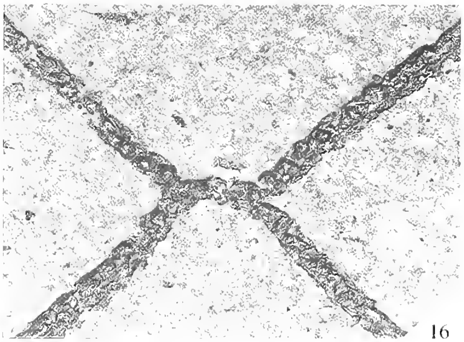
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WILLIAMS and STEVENS, *Kiaerograptus*, *Paratemnograptus*

Material and localities. Many flattened, non-isolated specimens from GP38; others from MPN17A, 17B. One possible poor isolated specimen from MPS42C.

Description. The rhabdosome consists of two slender stipes occasionally reaching over 35 mm long; second order branching has not been observed in our material. The stipes are 0·3–0·5 mm (commonly 0·4 mm) wide at th1^1, increasing only slightly to a maximum 0·5 mm (cf. type material). Narrow widths are probably due to preservation in oblique orientation, the larger measurements probably being more representative of the true widths.

The sicula is 1·0–1·15 mm long (cf. 1·4 mm for type material), is usually inclined rather then perpendicular to the stipes, and has a gentle convex curvature with respect to the rutellar margin. The aperture shows a pronounced rutellum and is typically 0·25 mm wide. Th1^1 presumably buds from the prosicula, growing down along the rutellar margin for 0·75–0·85 mm before turning sharply out and growing slightly downwards for the remainder of its 0·6–0·8 mm length. The base of the rutellar margin of the sicula is left free for 0·15–0·4 mm (commonly 0·2 mm), whereas the ventral wall of th1^1 subtends an angle of 60–80° with the sicular axis. The sicular bitheca has not been observed unequivocally, but by comparison with other taxa is almost certainly present. One specimen appearing to show a sicular bitheca reveals it to extend only slightly beyond the point where the ventral wall of th1^1 diverges from the sicula, probably explaining its cryptic form.

Th1^2 buds from th1^1 high on the reverse side, growing initially across the sicula in an almost horizontal direction before turning down to run along the antirutellar margin. It remains in contact with this margin until the sicular aperture is reached, at which point th1^2 bends abruptly out, subtending an angle of 50–60° with the sicular axis. This angle is maintained for 0·6–0·9 mm until the aperture is reached.

Remaining autothecae are almost straight, inclined at 10–15° with the dorsal stipe margin, but with a slightly concave ventral wall and gently flared aperture in most specimens. Occasionally, however, the ventral wall is straight; it is possible that the flaring is a preservational artefact related to differential lateral spread on flattening. Apertures are simple but deep, occupying one half to two-thirds of total stipe width. Thecal overlap represents a little under one half total thecal length, while thecal density is an almost constant 8–10 in 10 mm throughout the rhabdosome. Autothecal length appears to be related to size of rhabdosome, but it is unclear whether thecal growth is continuous throughout astogeny as demonstrated for several Arenig dichograptids by Williams and Stevens (1988*a*). Bithecae have not been observed apart from that of the sicula, and it is unlikely that they existed.

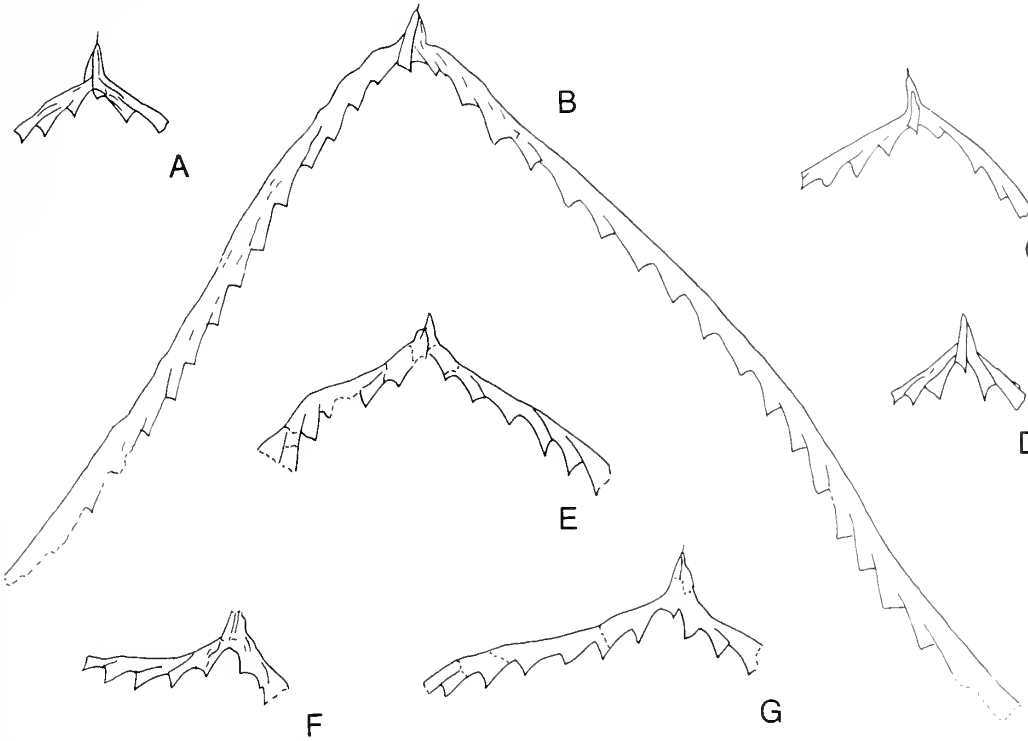
Remarks. Erdtmann *et al.* (1987) referred *K. pritchardi* to their new genus *Paradelograptus*; this genus is, however, characterized by slender thecae similar to *Adelograptus* and *Kinnegraptus* and lacks a sicular bitheca.

K. pritchardi appears to be a well-defined, consistent species with little variation in rhabdosome form and dimensions, in contrast to most other coeval taxa. It is easily separated from these by its distinctive proximal region. The Newfoundland representatives of *K. pritchardi* have rather smaller dimensions than those recorded by Berry (1966) for the type specimens. Berry recorded proximal widths of 0·7–0·8 mm widening to a maximum 0·8–0·9 mm in his text descriptions, but measurements from his illustrations and Cooper's (1979*a*, fig. 17*k*) figure of the lectotype demonstrate proximal widths of 0·6 mm. As noted above, thecal length (and consequently stipe width) appears to have increased during growth of the rhabdosome. As the type specimens have much longer stipes than our specimens, stipe widths between the two populations are considered to be compatible, while thecal densities are identical. The length of the sicula does, however, appear to be consistently longer in the type material (1·4 mm) than in the Newfoundland specimens (1·0–1·15 mm).

The single specimen of *Didymograptus tenuiramis* figured by Obut and Sobolevskaya (1962) is poorly preserved and seems to have suffered tectonic deformation. It does, however, appear very similar to *K. pritchardi* and is here tentatively referred to this species. Although Obut and Sobolevska (1962, fig. 4) refer the interval yielding *D. tenuiramis* to earliest Arenig, the associated assemblage could equally well be placed in the late Tremadoc as it contains '*Temnograptus*' species and predates the first occurrence of *T. approximatus.*

Specimens from the Yukon, northern Canada which Jackson (1974) referred to a new species *Didymograptus*(?) *stelki*, agree even more closely with the Australian types of *K. pritchardi* than those from Newfoundland, and we have no hesitation in assigning them to this species.

Most of our specimens of *K. pritchardi* originate from Green Point, where the late Tremadoc interval is represented by a succession of fine-grained, fissile shales deposited in a rather deeper, more distal environment than elsewhere in the Cow Head Group. This distribution may be related to original environmental restraints, or may be due to poor preservation in rather coarser lithologies elsewhere. A similar problem exists for slender Arenig graptoloids in the Cow Head group, *Kinnegraptus* and *Adelograptus* being largely restricted to the more distal, fine-grained facies, deposited in deeper water.



TEXT-FIG. 7. *Kiaerograptus* cf. *K. taylori* (T. S. Hall, 1899), × 5. A–D, GP38; A, GSC 87369; B, GSC 87386; C, GSC 87392; D, GSC 87410. E–G, MPS42C; E, GSC 87356; F, GSC 87357; G, GSC 87358.

Kiaerograptus cf. *K. taylori* (T. S. Hall, 1899)

Text-fig. 7A–G

cf. 1899 *Didymograptus taylori*, n. sp.; T. S. Hall, pp. 167–168, pl. 17, figs 11 and 12.
cf. 1960 *Didymograptus taylori* T. S. Hall; Thomas, pl. 1, fig. 15.

Material and localities. Seven flattened, non-isolated specimens from GP38 and MPS42C.

Description. The rhabdosome is composed of two stipes up to 25 mm long, with a deflexed or declined form and separated by an angle of 90–120°. They measure 0·6–0·8 mm wide at the first thecal aperture; the larger width is found in specimens with longer thecal lengths and higher inclinations to the dorsal stipe wall, but may be related to lateral spread in some instances. The stipes soon attain their maximum width of 1·0 mm, which is then maintained throughout the rhabdosome.

The sicula is a consistent 1·5–1·6 mm long, with an apertural width of 0·3–0·45 mm. It is initially straight, but has a convex curvature with respect to the rutellar margin over the distal 0·5 mm. A short nema is occasionally present; the sicular bitheca has not been seen, but is almost certainly present. Proximal development has not been observed, but is probably similar to other late Tremadoc graptolites with a prosicular origin for th1^1. With the exception of the sicula, bithecae appear to be absent.

Autothecae have a low initial inclination of about 10° to the dorsal margin, but this increases throughout their length to reach a maximum of 30–40° near the aperture. Thecal length is somewhat variable; overlap is about one half of total length in early thecae, reducing to about one third distally. Free ventral thecal margins are markedly concave, particularly towards the apertures which occupy one third to one half of total stipe width, giving a markedly denticulate appearance to the ventral stipe margin. Thecal density is somewhat variable 8–10 in 10 mm proximally, but reduces to a constant 8 in 10 mm distally.

Remarks. Although the generic assessment of *K. taylori* has been discussed relatively recently (e.g. by Cooper and Stewart 1979, p. 790), no additional specimens appear to have been described since the original description by T. S. Hall in 1899. From his remarks (1899, p. 168) it seems that Hall possessed more than the one specimen illustrated; unfortunately there are several discrepancies between his written description, figure at natural size and the illustration recorded as ×3 magnification. Thomas (1960, fig. 15) has since provided a rather clearer figure of the specimen at natural size.

Because of Hall's poor original description and lack of revisions using the type material, assignment of our Newfoundland specimens cannot be certain and we therefore refer them to *K.* cf. *taylori*. This species is unlike any other taxa from the late Tremadoc of the Cow Head Group, with the exception of *K. pritchardi*, from which it differs by its longer sicula, more robust form, steeply inclined stipes and narrower thecal apertures. Bulman (1950) compared his new species *Didymograptus primigenius* with *D. taylori*; the overall dimensions and rhabdosome form of this taxon from the middle Tremadoc of Quebec are, however, closer to those of *K. pritchardi*. It is distinguished from this species by its more steeply inclined thecae and higher thecal density of 11 in 10 mm.

Kiaerograptus undulatus sp. nov.

Plate 1, figs 2–4; Plate 3, figs 1 and 2; Text-fig. 8A–H

cf. 1937 *Didymograptus norvegicus*, n. sp.; Monsen, pp. 176–177, pl. 2, figs 7 and 8; pl. 4, figs 4 and 5; fig. 6.

1983 ?*Kiaerograptus* sp. cf. *K. quasimodo* Rushton; Henderson, p. 155, fig. 5*g–j*.

Derivation of name. From *undulatus* (Latin) meaning 'wavy', referring to the folded dorsal stipe margin.

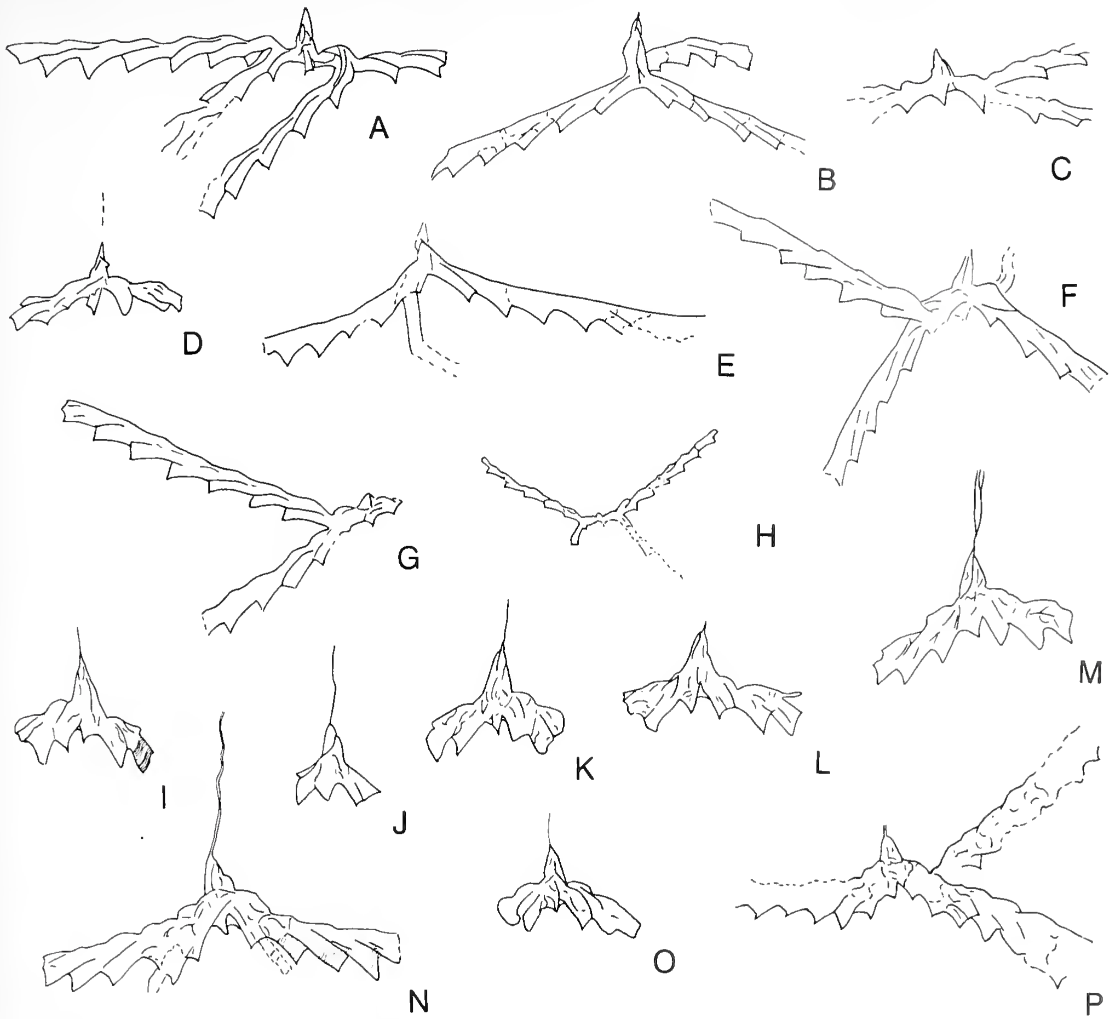
Type specimen. The holotype is GSC 87413, from Green Point (GP40). Figured Text-figure 8A.

Diagnosis. Small rhabdosome composed of four (occasionally two or three) slightly declined, radiating stipes, measuring 0·7–0·8 mm wide proximally with rapid increase to the maximum 1·0 mm. Sicula 1·5–1·8 mm long, almost straight, with apertural width of 0·25 mm. Prominent sicular bitheca filling much of 'notch' of basal rutellar margin. Autothecae strongly curved, with strong prothecal folds, wide apertures occupying one half of total stipe width and numbering 9–10 in 10 mm. Many or all autothecae with bithecae opening into large apertures.

Material and localities. Fifteen flattened, non-isolated specimens from GP38, 40; MPS42C; CH8·34. One isolated, three-dimensional specimen from MPS42C.

Description. The species is known only from small proximal fragments with stipes up to 8 mm long. The rhabdosome typically consists of four, gently declined, radiating stipes, formed by the dichotomous division of th2^1 and 2^2. Occasional specimens with two horizonal stipes considered to belong to this species have, however, been found. Stipes are generally 0·7–0·8 mm wide proximally, with rapid increase to 1·0 mm, although a few specimens are 1·0 mm wide proximally. The dorsal stipe margin is characterized by pronounced prothecal folds, although these are less conspicuous in more poorly preserved, flattened material.

The sicula is 1·5–1·8 mm long and almost straight throughout its entire length, with an apertural width of 0·25 mm. Proximal development has not been observed clearly, but evidently agrees with that of other late



TEXT-FIG. 8. A–H, *Kiaerograptus undulatus* sp. nov., A–G × 5, H × 2·5. A, GSC 87413, Holotype, GP40. B, GSC 87296, CHN8.34. C, GSC 87318, MPS42C. D, GSC 87328, MPS42C. E, GSC 87359, MPS42C. F, GSC 87371, GP38. G, GSC 87414, GP40. H, GSC 87322, MPS42C. I–P, *Kiaerograptus magnus* sp. nov. I–N GP38, × 5; I, GSC 87365; J, GSC 87404; K, GSC 87363; L, GSC 87372; M, GSC 87408; N, GSC 87361, Holotype (also figured Pl. 1, fig. 7). O, GSC 87330, MPS42C (also figured Pl. 1, fig. 3). P, GSC 87325, MPS42C.

Tremadoc taxa. Th1^1 diverges from the sicula relatively high, leaving the basal rutellar margin free for 0·5–0·6 mm. Much of this 'notch' is, however, commonly filled by the sicular bitheca, giving a more robust and 'filled-in' appearance to the proximal region. Th1^2 also leaves the sicula above the level of the sicular aperture, leaving the antirutellar margin free for 0·1–0·2 mm.

The free ventral margins of th1^1 and 1^2 measure 1·0 mm and 0·8 mm respectively; both show pronounced downward curvature throughout their free portions and splay out towards the apertures, which are 0·35–0·4 mm in diameter (half total stipe width). Th2^1 and 2^2 are commonly dichotomous, giving rise to the typically 'tetragraptid' form; in these specimens th1^1 and 1^2 possess bithecae which open into large apertures alongside those of the autothecae and directly below the point of branching. It is unclear whether these bithecae are present in the two-stiped forms, or whether they occur throughout the rhabdosome. End-on views of the single isolated specimen suggest that they are indeed present in at least the succeeding few thecae, unless this specimen is showing a third-order dichotomy. All autothecae throughout the rhabdosome show the same characteristic strong curvature, prothecal folds and wide apertures occupying one half of total stipe width. Thecal overlap is greater than one half, while thecal density is a constant 9–10 in 10 mm.

Remarks. K. undulatus is a very distinctive form when well preserved owing to the sinuous nature of the thecae, which gives an appearance reminiscent of the Arenig sinograptids. The outline of the dorsal wall is somewhat variable, from specimens with strong prothecal folds to others with an almost straight dorsal margin. Although this may be partly an original morphological feature, the folds may well have been reduced by differential lateral spread on compaction, as described for the Upper Ordovician *Dicellograptus complanatus* Lapworth by Briggs and Williams (1981) and Williams *et al.* (1982).

Henderson's (1983) specimens of *K.*? cf. *quasimodo* agree well with *K. undulatus*, although they are all two-stiped forms. The types of *K.*? *quasimodo* described by Rushton (1981) from the middle or upper Tremadoc subsurface of central England differ, however, by their longer sicula and more steeply inclined thecae, resulting in a slightly higher thecal count. Most specimens of *K.*? *quasimodo* were two-stiped forms, although one possible three-stiped specimen with a higher thecal density was recorded by Rushton (1981, fig. 3*c*). *K.*? *quasimodo* is clearly similar to *K. undulatus* and may well represent an ancestral taxon. *K. undulatus* is also comparable with *Didymograptus norvegicus* Monsen: this has a folded dorsal margin and equivalent thecal densities, but a rather smaller, inclined sicula 1·4 mm long and two reclined stipes.

The only other associated species with which *K. undulatus* may be confused is *K. bulmani* sp. nov. The latter species has a much more slender and open rhabdosome, rather more gently inclined thecae with a marginally lower thecal density of 8–9 in 10 mm, and seems to lack the prominent folded dorsal margin (although one two-stiped specimen possibly referable to this species does have prothecal folds).

Kiaerograptus magnus sp. nov.

Plate 1, figs 5–7; Plate 3, figs 4 and 7; Text-fig. 7I–P

Derivation of name. From *magnus* (Latin) meaning 'large', in reference to the large and robust sicula and proximal region.

Type specimen. The holotype is GSC 87361, from Green Point (GP38). Figured Plate 1, fig. 7 and Text-figure 8N.

Diagnosis. Robust rhabdosome with four, three or two stipes 1·2 mm wide proximally. Sicula up to 2·3 mm long, almost straight, with pronounced rutellum and aperture 0·5 mm diameter. Autothecae simple, inclined at 30–40° to dorsal margin, numbering 9–10 in 10 mm. Bithecae apparently lacking with exception of large sicular bitheca.

Materials and localities. Ten flattened specimens from MPS42C and GP38. Four isolated, three-dimensional specimens from SP143 and MPS42C.

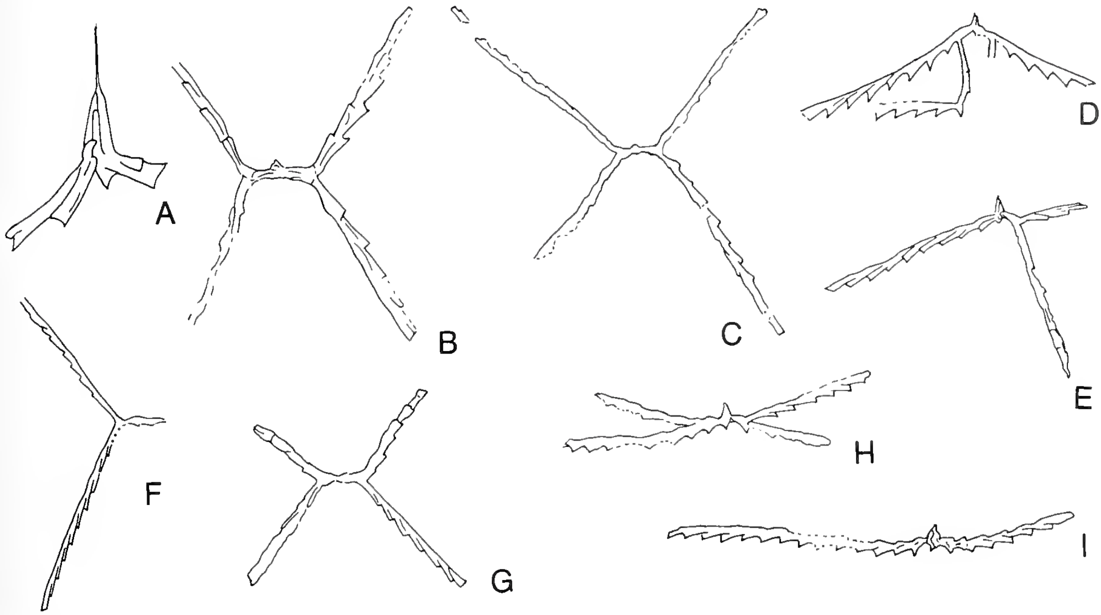
Description. The rhabdosome is robust with two, three or four stipes, 1·2 mm wide proximally and increasing rapidly to over 1·5 mm within 5 mm. Only proximal fragments have been positively identified, with stipes up to 6 mm long.

The sicula is long and wide, reaching up to 2·3 mm long measured along the gently convex rutellar margin, with a conspicuous rutellum projecting 0·2 mm and long nema which is occasionally thickened or forked (Text-fig. 8M, N). The sicula is 0·5 mm diameter at its aperture. Th1^1 buds from the prosicula, growing down in contact with the metasicula for about 1 mm before diverging gently out at 20–30°. A large sicular bitheca fills most of the notch left between the rutellar margin of the sicula and ventral wall of th1^1. The arrangement of the sicula and first theca is highly symmetrical in young growth stages, giving an appearance approaching that found in the Arenig genus *Isograptus*. This symmetry is, however, lost during astogeny, as th1^1 continues to grow with a free ventral wall up to 1·1 mm long.

Th1^2 buds from high up th1^1, as does Th2^1. It grows down and across the sicula, its ventral wall intersecting the antirutellar apertural margin of the sicula. Its original angle of 30° subtended with the sicular axis decreases slightly throughout its distal portion, resulting in a concave free ventral margin up to 1·0 mm long.

Remaining development is similar to other *Kiaerograptus* taxa, th2^1 and 2^2 normally being dichotomous, although one or both dichotomies may be suppressed. Remaining autothecae are straight and inclined at 30–40° to the dorsal margin. They overlap about one half their length, have simple apertures occupying about one half of total stipe width, and number 9–10 in 10 mm. No bithecae have been observed apart from that of the sicula.

Remarks. The robust proximal region and large sicula separate *K. magnus* from all other coeval *Kiaerograptus* species and give an appearance reminiscent of *Clonograptus*. However, *K. magnus* lacks the common bithecae characteristic of this genus during the late Tremadoc, and appears to only have a maximum of four stipes, although more complete specimens might potentially possess further delayed, dichotomous branching. The forked and thickened nemata present on some specimens are unusual for graptolites from this stratigraphical interval and may have some taxonomic significance.



TEXT-FIG. 9. A–H, *Kiaerograptus bulmani* (Thomas, 1973). A, GSC 87400, GP38, × 10. B, GSC 87420, GP40, × 5. C–H, × 2·5; C, GSC 87324, MPS42C; D, GSC 87339, MPS42C; E, GSC 87295, CHN8.34; F, GSC 87364, GP38; G, GSC 87366, GP38; H, GSC 87319, MPS42C. I, *K. bulmani* (Thomas, 1973)?, GSC 87323, MPS42C, × 2·5.

Kiaerograptus bulmani (Thomas, 1973)

Plate 1, figs 8 and 9; Plate, 3 figs 5, 6, 8–14; Text-fig. 9A–I

1971	*Tetragraptus otagoensis* (Benson and Keble); Erdtmann, pp. 259–260, pl. 33, figs 1–3.
1973	*Tetragraptus bulmani* sp. nov.; Thomas, pp, 530–531, pl. 2, figs *b* and *c*.
1979	*Tetragraptus bulmani* Thomas; Cooper and Stewart, p. 795, text-fig. 8*h*, *k*.

Type specimen. The holotype is specimen No. 64419 in the Mines Department Museum, Melbourne. From the middle Lancefieldian (La2), loc. 68, Staurograptus Gully, Parish of Springfield, Victoria.

Diagnosis (revised, incorporating descriptions by Thomas (1973) and Cooper and Stewart (1979)). Small, slender rhabdosome with four or three, radiating, gently declined stipes increasing from 0·4–0·5 mm wide proximally to a maximum 0·8 mm (0·5–0·6 mm in scalariform or oblique preservation). Thecae simple, straight, gently inclined at about 20° and numbering a constant 8–10 in 10 mm. Sicula with bitheca, other bithecae apparently lacking except at dichotomies.

Material and localities. Twenty flattened specimens from CH8·34; MPS42C; GP38, 40. Fifteen isolated, three-dimensional specimens from SPI43, MPS42C and GP38.

Description. The rhabdosome is composed of four radiating, slender stipes up to 20 mm long. Proximally they have a dorso-ventral width of 0·4–0·5 mm, increasing to 0·5–0·7 mm in 5 mm and reaching a maximum of 0·8 mm. Stipes are commonly preserved in oblique or scalariform view, resulting in rather narrower widths of 0·5–0·6 mm. Rare preservation of the rhabdosome in lateral view reveals the stipes to be gently declined. Occasionally one dichotomy is suppressed, resulting in a three-stiped rhabdosome, although the majority of specimens from the Cow Head Group possess four stipes. One specimen possibly referable to *K. bulmani* (Text-fig. 9I) has only two, horizontal stipes, suggesting suppression of both dichotomies; this example however has a strongly folded dorsal margin and may not belong to this species.

The sicula is 1·4 mm long (but apparently only 1·2 mm in non-isolated specimens), measured along the rutellar margin, with an apertural diameter of 0·2–0·25 mm. It is straight or almost straight throughout its length, with a small but conspicuous rutellum projecting 0·08 mm beyond the antirutellar, apertural margin. Th1^1 buds from the prosicula on the rutellar side and grows down in contact with the sicula for 0·8–0·85 mm before turning out, after which it subtends an angle of 40° with the sicular axis for the remaining 0·7–0·9 mm of its length. Th1^1 has an almost constant diameter of 0·2–0·23 mm during the second portion of its development and opens into a simple aperture.

A sicular bitheca is invariably present, opening at a level varying from 0·15 mm above the point of divergence of th1^1 to just below the level of divergence. Development may be sinistral or dextral. Th1^2 buds from th1^1 about 0·5 mm below the apex of the sicula; it grows down and across at 30° to the sicular axis, maintaining this direction of growth throughout its length. Subsequent development and branching patterns appear to be typically 'dichtograptid', with th1^2, th2^1 and th2^2 dichotomous (one or both branchings may be suppressed). Bithecae appear to be absent apart from that of the sicula, and possibly at dichotomies (Plate 3, fig. 13).

Remaining thecae are simple, straight, gently inclined at about 20° to the dorsal margin and have apertures occupying one third to one half of total stipe width. Thecal overlap is about one-third, while thecal density is a uniform 8–10 in 10 mm throughout the rhabdosome. Rare flattened specimens appear to exhibit prothecal folds, but these are not present in isolated material. Critical observation suggests that they may be due to lateral spread of the apertural regions during flattening in oblique or scalariform orientation, apertural walls becoming visible on both sides of the stipe margin (e.g. Text-fig. 9B, G).

Remarks. K. bulmani is distinct from other taxa at this stratigraphical level due to its narrow stipes and widely spaced thecae. Our specimens appear to agree with the Australian types in all respects, except in lacking flared thecal apertures. Such flaring is, however, common in many graptolites with straight, simple thecae, due to post-mortem, differential lateral spread during flattening of the rhabdosome and is, therefore, of no taxonomic importance. *K. bulmani* differs from *Kiaerograptus otagoensis* (Benson and Keble, 1936) by its rather narrower stipes and lower thecal densities; Erdtmann's (1971) specimens referred to *K. otagoensis* are from Martin Point and clearly belong to *K. bulmani. K. bulmani* may be distinguished from *K. undulatus* sp. nov. by that species' rather different proximal development, wider stipes and prominent prothecal folds. Occasionally, however, specimens are found preserved in oblique or scalariform orientation which could be assigned to either one of the species.

The similarity in thecal style between *K. bulmani* and *Kiaerograptus pritchardi* (T. S. Hall) was noted both by Thomas (1973) and by Cooper and Stewart (1979). Our isolated and flattened material reveals that *K. bulmani* has a similar proximal development to that shown by both *K. pritchardi* and *K. taylori*, which is why we refer that species to *Kiaerograptus* rather than retaining within the dichograptid genus *Tetragraptus. K. otagoensis* is also similar and should be referred to this genus. Cooper and Stewart (1979) remarked that *K. bulmani* was rather similar to the

Bendigonian (lower Arenig) species *Tetragraptus harti* T. S. Hall. Williams and Stevens (1988*a*) recently redescribed this taxon from the *D. bifidus* Zone of the Cow Head Group and transferred it to the genus *Etagraptus*. Although similar in overall rhabdosome form, *E. harti* is a true dichograptid without a sicular bitheca, and any similarity to *K. otagoensis* is entirely homoeomorphic.

Genus PARATEMNOGRAPTUS nov.

Type species. Paratemnograptus isolatus sp. nov. By monotypy.

Diagnosis. Pauciramous, radiate rhabdosome with up to sixteen stipes arising from two primary stipes by three orders of widely spaced, delayed, irregular, dichotomous branching. Sicula with bitheca. Autothecae gently curved with moderate inclination, simple apertures and apparently lacking bithecae.

Remarks. Proximal branching conforms to a standard tetragraptid plan, with two primary stipes and $th2^1$ and $th2^2$ dichotomous. Subsequent dichotomies are delayed and irregular, many large rhabdosomes possessing only four stipes. Overall form may, therefore, be similar to either *Tetragraptus* or *Temnograptus*, although both these genera are Arenig in age and lack bithecae. *Paratemnograptus* further differs from the diagnosis of *Temnograptus* given by Bulman (1970, p. V113) in having irregular dichotomous stipe division and non-denticulate thecae. The type species of *Temnograptus*, namely *T. multiplex* (Nicholson, 1868), is poorly known and based on inadequate, flattened and deformed material from an uncertain stratigraphic level. Further work may ultimately prove *Paratemnograptus* to be synonymous with Nicholson's genus.

Paratemnograptus isolatus sp. nov.

Plate 1, figs 10–16; Plate 2, fig. 4; Plate 4, figs 1–8; Text-fig. 10A–O

?1899 *Tetragraptus decipiens*, n. sp.; T. S. Hall, pp. 168–169, pl. 17, figs 13–15; pl. 18, figs 16–19.
?1904 *Temnograptus noveboracensis* sp. nov.; Ruedemann, pp. 619–620, pl. 5, figs 15–20, 35, 36.
?1920 *Tetragraptus decipiens*, T. S. Hall; Keble, pp. 199–200, pl. 34, fig. 1*a–e*.
?1947 *Temnograptus noveboracensis* Ruedemann; Ruedemann, p. 284, pl. 44, figs 14–16; pl. 45, figs 1–4.
?1962 *Temnograptus* aff. *noveboracensis* Ruedemann; Obut and Sobolevskaya, p. 79, pl. 3, fig. 3.
?1966 *Tetragraptus decipiens* T. S. Hall; Berry, pp. 423–424, pl. 44, figs 5, 10, 11.
?1969 *Tetragraptus decipiens* T. S. Hall; Bulman and Cooper, pp. 215–216, pl. 1, figs 1–4; fig. 3*a–c*.
?1974 *Clonograptus* sp. A; Jackson, pp. 46–47, text-fig. 4.
1974 *Clonograptus* sp. B; Jackson, p. 47, text-fig. 1*m*, *n*.
?1974 *Tetragraptus decipiens* T. S. Hall; Jackson, pp. 53–54, pl. 5, fig. 4.
1979*a* *Temnograptus* aff. *regularis* (Törnquist, 1904); Cooper, p. 58, pl. 1*f*; fig. 24.
?1979*b* *Tetragraptus decipiens* T. S. Hall; Cooper, fig. 5*f*.
1979 *Temnograptus* sp.; Cooper and Stewart, pp. 793–795, text-fig. 8*c*.
?1979 *Tetragraptus decipiens* T. S. Hall; Cooper and Stewart, pp. 795–796, text-fig. 8*a*, *b*.
?1982 *Temnograptus* sp.; Gutierrez-Marco, fig. 2*k*.

Derivation of name. From *isolatus* (Latin) meaning detached or separate, in reference to the widely spaced, irregular dichotomous branching.

Type specimen. The holotype is GSC 87284, from the Ledge, Cow Head Peninsula (CHN8.30). Figured Text-fig. 10L.

Diagnosis. Large rhabdosome with four to sixteen slightly flexuous, radiating stipes increasing rapidly from 0·8–1·2 mm wide proximally to 1·4 mm maximum. Slender sicula with sicular bitheca, funicle composed of th1^1 and th1^2 2·5–3·0 mm wide. Thecae simple, overlap one half, thecal density 9–10 in 10 mm.

Material and localities. Numerous flattened specimens from CHN8.30; MPN17B; MPS42C; GP38, 40. Over twenty isolated, three-dimensional specimens from SPI43, MPS42C.

Description. The rhabdosome consists of four to sixteen long, slightly flexuous, radiating stipes reaching over 70 mm long and widening rapidly from 0·8–1·2 mm proximally to a maximum 1·4 mm which is then maintained.

The sicula is 1·6–1·8 mm long; it is straight throughout its length and relatively slender, reaching 0·2 mm diameter at the aperture. It has a small but conspicuous rutellum extending 0·1–0·15 mm beyond the antirutellar margin. Th1^1 generally buds from the prosicula on the rutellar margin, although in one well-preserved specimen it buds from the antirutellar side, then swings immediately across to the rutellar margin. Th1^1 grows down along the rutellar margin for 0·75 mm before turning outwards, subtending an angle of 40° with the sicular axis which is maintained throughout the remainder of its length. The distal rutellar margin of the sicula is left free for 0·25–0·3 mm. A sicular bitheca buds from the sicula below the point of origin of th1^1, opening into an aperture a little above the point of divergence of the ventral wall of th1^1 from the sicula. Development may be either right- or left-handed; th1^2 buds from th1^1 above its point of deflection, growing down and across the sicula and the ventral wall of th1^2 intersects the base of the antirutellar sicula margin. Th1^2 is dichotomous, giving rise to th2^1 and th2^2, as are each of these subsequent thecae to give the typical 'tetragraptid' proximal plan. The funicle, consisting of the first two thecae, is 2·5–3·0 mm wide.

Subsequent autothecae have a typically dichtograptid appearance; their angle of inclination with the dorsal margin increases from 30° initially to 50° towards the aperture, which is simple. Thecal overlap is one half of total length, while apertures occupy one half to two-thirds of total stipe width. Bitheca appear to be lacking with the exception of the sicular bitheca. Thecal density is a uniform 9–10 in 10 mm throughout the rhabdosome.

Remarks. Although the overall form is distinctive, details of thecal morphology or proximal development are rarely seen in flattened specimens owing to common preservation in scalariform orientation. Most rhabdosomes have only four stipes, but sufficient specimens have been found with additional distal dichotomies to determine the variability of this morphological feature. There are no other associated species which might be confused with *P. isolatus*; as can be seen from the list of synonymies, both the generic and specific identity of this taxon have, however, been problematic.

Temnograptus regularis (Törnquist) as described by Törnquist (1904) and Monsen (1937) certainly appears similar, but both our material and that described by Cooper (1979*a*) has more widely spaced dichotomies, more slender stipes and is much earlier (late Tremadoc as opposed to middle Arenig).

Temnograptus noveboracensis Ruedemann was based entirely on distal stipe fragments and is, therefore, not a strictly valid taxon. Ruedemann (1947, pl. 44, figs 14–16) did, however, figure three fragments from the Cow Head Group and these are likely to belong to *P. isolatus*.

Tetragraptus decipiens T. S. Hall has been recorded previously from the late Tremadoc and early

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EXPLANATION OF PLATE 2

Fig. 1. *Aorograptus victoriae* (T. S. Hall, 1899). GSC 87309, MPS42C, ×2·5 (also figured Text-fig. 11L).

Figs 2 and 3. *Adelograptus* cf. *A. tenellus* (Linnarsson, 1871). 2, GSC 87376, GP38, ×5. 3, GSC 87307, MPN17B, ×10.

Fig. 4. *Paratemnograptus isolatus* gen. et sp. nov. GSC 87362, GP38, ×10 (also figured Text-fig. 10B).

Fig. 5. *Clonograptus* sp. B. GSC 87314, MPS42C, ×2·5 (also figured Text-fig. 15J).

Fig. 6. *Clonograptus* sp. A. GSC 87354, MPS42C, ×2·5.

Figs 7–11. *Rhabdinopora* sp. 7, GSC 87308, MPN17B, ×10. 8, GSC 87290, CHN8.30, ×5. 9, GSC 87291, CHN8.30, ×2·5. 10, GSC 87396, GP38, ×5. 11, GSC 87292, CHN8.30, ×2·5. 13, GSC 87293, CHN8.30, ×2·5.

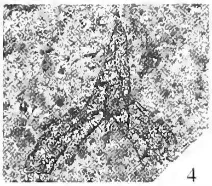
Fig. 12. Dendroid indet., distal fragment. GSC 87316, MPS42C, ×5.

PLATE 2


1


2


3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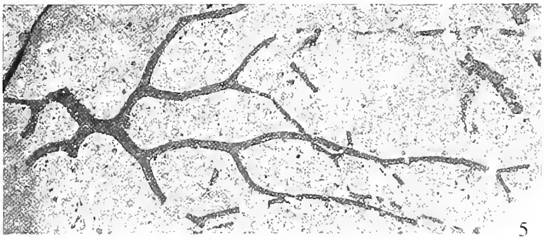
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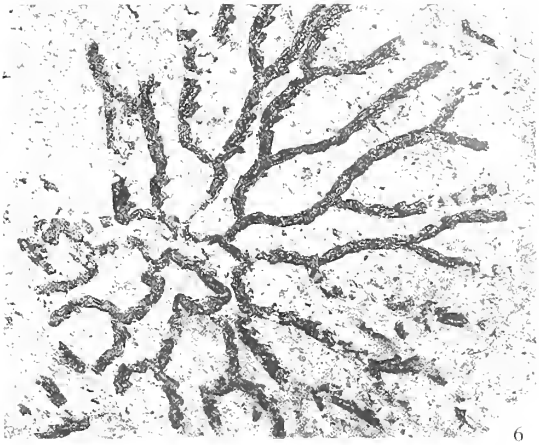
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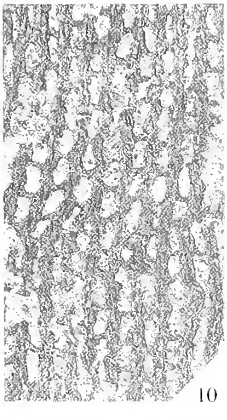
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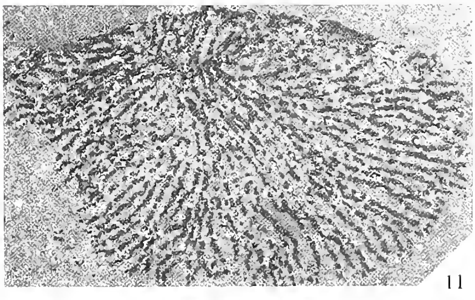
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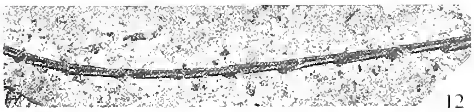
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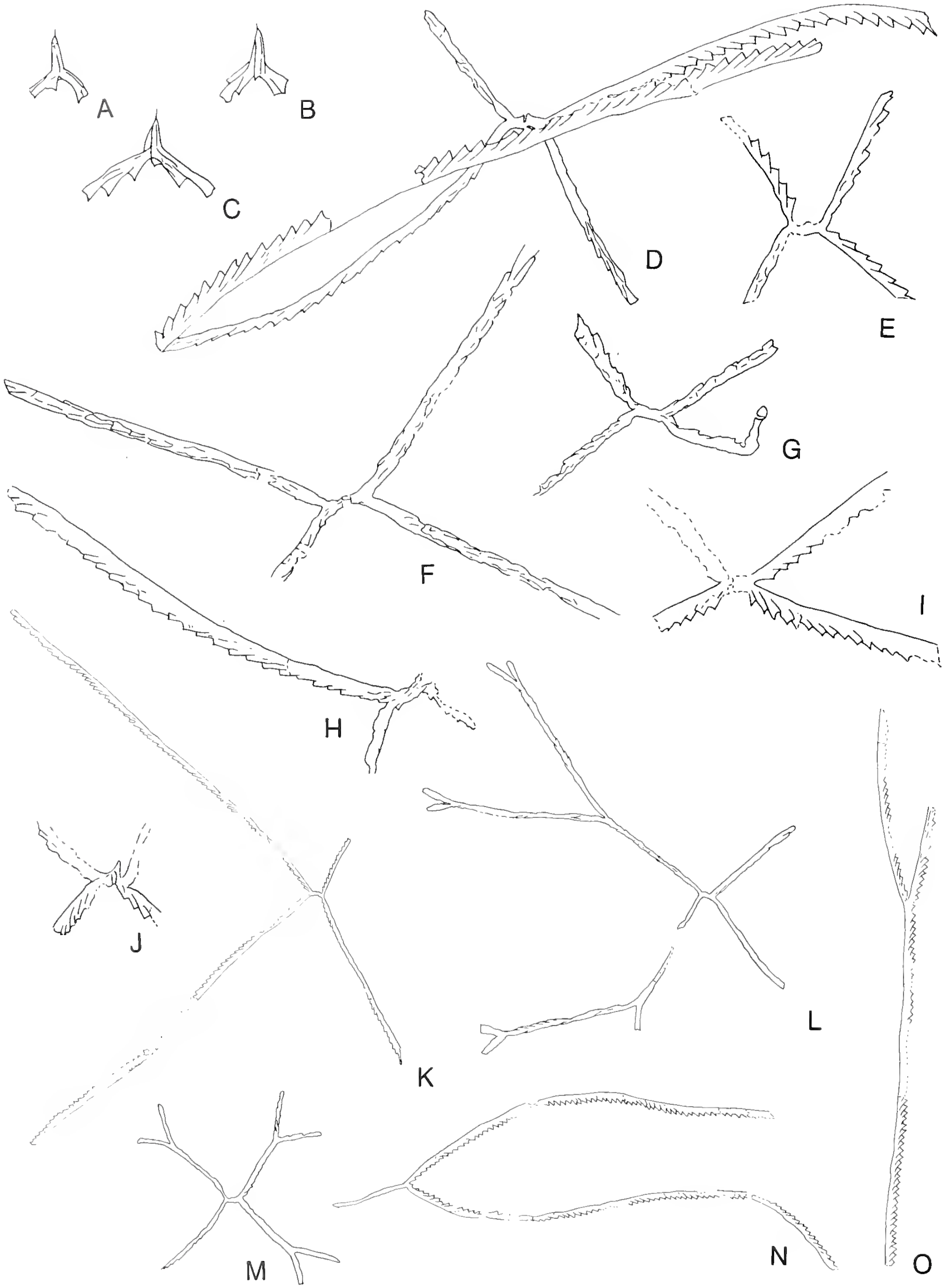
13

WILLIAMS and STEVENS, Late Tremadoc graptolites



TEXT-FIG. 10. For legend see opposite.

Arenig of Australasia and North America; the type specimens are, however, poor and are only juveniles (see Berry 1966). The only description of *T. decipiens* including anything more than juveniles was by Keble (1920). The taxonomic affinities of *T. decipiens* were discussed by Williams and Stevens (1988*a*), who concluded that many lower Arenig specimens were probably juvenile representatives of *T. approximatus approximatus* Nicholson. We furthermore believe that the Tremadoc examples of *T. decipiens* are probably juvenile representatives of our new species *P. isolatus*, in which case *T. decipiens* would be a senior synonym. The dimensions of the sicula given by Berry (1966) for the types of *T. decipiens* are, however, greater than those for *P. isolatus*; he recorded that the sicula was 1·9–2·4 mm long and 0·4–0·5 mm wide at the aperture (cf. 1·6–1·8 mm long and 0·2 mm wide for *P. isolatus*).

Until a better population of *T. decipiens* is collected from the type locality, including large, mature rhabdosomes and specimens in which the presence or absence of a sicular bitheca can be determined, the synonymy with *P. isolatus* must remain questionable.

Genus AOROGRAPTUS nov.

Derivation of name. From *aoros* (Greek), meaning pendulous, hanging or waving, in reference to the pendent nature of the rhabdosome.

Type species. *Bryograptus victoriae* T. S. Hall, 1899, p. 165, pl. 17, figs 1 and 2.

Diagnosis. Pendent or declined rhabdosome with regular, commonly delayed, dichotomous branching from two primary stipes. Sicula and most autothecae with bithecae; autothecae composed of simple, dichgraptid-like tubes, commonly curved with fairly high distal inclinations, stipes relatively robust.

Remarks. Until more extensive taxonomic revision of Middle and Upper Tremadoc graptolites is accomplished, this genus is essentially monotypic. *A. victoriae*, the type species, has been previously assigned to both *Bryograptus* and *Adelograptus*. It differs from the former genus by having two, rather than three, primary stipes, and from the latter in having a relatively robust, large rhabdosome with regular branching. When preserved in radiate, rather than pendent, orientation, the rhabdosome gives an appearance which would normally have been referred to *Clonograptus*. As discussed elsewhere, we consider this genus to be a typically dichograptid, Arenig genus, lacking bithecae or any other 'dendroid' features (in the traditional sense). It is therefore likely that many specimens referred previously to *Clonograptus* are actually representatives of our new genus *Aorograptus* preserved in radiate (horizontal) orientation.

Several previous authors have referred to the possibility that *Bryograptus* evolved to give the lower Arenig dichograptid genus *Pendeograptus* and/or the pendent didymograptids (see Fortey and Cooper 1986 for discussion). In our opinion, it is likely that *Aorograptus* evolved from *Bryograptus* in the late Tremadoc through loss of one primary stipe and the stolon system, then subsequently gave rise to *Pendeograptus* through loss of bithecae and further stipe reduction. It is not, however, the ancestor of *Didymograptus* (*Didymograptellus*) Cooper and Fortey, 1982, which almost certainly evolved from the *Didymograptus* (*Expansograptus*) *nitidus* group of extensiform didymograptids (see Williams and Stevens 1988*a*).

TEXT-FIG. 10. *Paratemnograptus isolatus* gen. et sp. nov., A–C × 5, D–J × 2·5, K–O × 1. A, GSC 87301, MPN17B. B, GSC 87362, GP38 (also figured Pl. 2, fig. 4). C, GSC 87370, GP38. D, GSC 87333, MPS42C. E, GSC 87402, GP38. F, GSC 87280, CHN8.30. G, GSC 87281, CHN8.30. H, GSC 87382, GP38. I, GSC 87282, CHN8.30. J, GSC 87283, CHN8.30. K, GSC 87355, MPS42C. L, GSC 87284, Holotype, CHN8.30. M, GSC 87334, MPS42C. N, GSC 87415, GP40. O, GSC 87311, MPS42C.

Aorograptus victoriae (T. S. Hall, 1899)

Plate 2, fig. 1; Plate 3, fig. 15?; Plate 4, figs 9–14; Plate 5, figs 1–8; Text-fig. 11A–Q

1899*a* *Bryograptus victoriae*, n. sp.; T. S. Hall, p. 165, pl. 17, figs 1 and 2.
1899*a* *Bryograptus clarki*, n. sp.; T. S. Hall, pp. 165–166, pl. 17, figs 3 and 4.
1899*b* *Bryograptus victoriae*; T. S. Hall, p. 450, pl. 22, figs 11 and 12.
1914 *Bryograptus* sp.; T. S. Hall, pl. 8, figs 5 and 6.
1932 *Bryograptus victoriae* T. S. Hall; Harris and Keble, pl. 4, fig. 2.
1933 *Bryograptus pauxillus sp. nov.*; Benson, p. 403 (*nom. nud.*).
1936 *Bryograptus hunnebergensis* Moberg; Benson and Keble (*pars*), pp. 269–270, pl. 30, figs 1–11 (*non* pl. 30, figs 14 and 15 = *A.* cf. *tenellus* (Linnarsson)?).
?1936 *Bryograptus simplex* Törnquist; Benson and Keble, p. 270, pl. 30, figs 12 and 13.
1938*b* *Bryograptus victoriae* T. S. Hall; Harris and Thomas, pl. 1, fig. 7.
1938 *Bryograptus clarki* T. S. Hall; Harris and Thomas, pl. 1, fig. 8.
1941 *Adelograptus victoriae* (T. S. Hall); Bulman, p. 115 (no description or figures, but refers to *Adelograptus* and synonymises *A. clarki*).
1955 *Adelograptus asiaticus*; Mu, p. 30, pl. 10, figs 4–7.
?1955 *Adelograptus sinicus*; Mu, p. 30, pl. 10, fig. 8.
1960 *Bryograptus victoriae* T. S. Hall; Thomas, pl. 1, fig. 6.
1960 *Bryograptus clarki* T. S. Hall; Thomas, pl. 1, fig. 7.
?1960 *Adelograptus victoriae* (T. S. Hall); Berry, pp. 46–47 (remarks only, no descriptions or figures).
1966 *Adelograptus clarki* (T. S. Hall); Berry, pp. 419–421, pl. 44, figs 2 and 4.
1966 *Adelograptus victoriae* (T. S. Hall); Berry, pp. 421–422, pl. 44, fig. 1.
1968 *Adelograptus kazakhstanensis* Tzaj, n. sp.; Tzaj, pp. 493–494, pl. 5, fig. 2.
1968 *Bryograptus ulutanensis* Tzaj, n. sp.; Tzaj, p. 495, pl. 5, fig. 3.
1969 *Bryograptus*? sp. of T. S. Hall; Bulman and Cooper, fig. 4*a*, *b*.
1974 *Adelograptus victoriae* (T. S. Hall); Jackson, p. 45, pl. 5, fig. 2; text-fig. 2*a*.
1974 *Adelograptus kazakhstanensis* Tzaj; Tzaj, pl. 37, pl. 1, figs 6 and 7.
1974 *Bryograptus ulutanensis* Tzaj; Tzaj, pp. 38–39, pl. 2, figs 1–3; fig. 4.
1974 *Bryograptus* sp.; Tzaj, p. 39, pl. 2, fig. 4.
1979*a* *Adelograptus clarki* (T. S. Hall); Cooper, pp. 54–55, pl. 2*a*, *b*; fig. 19*a*–*c*.
1979*b* *Adelograptus victoriae* (T. S. Hall); Cooper, fig. 5*g*.
1979 *Adelograptus victoriae* (T. S. Hall); Cooper and Stewart, pp. 784–785, text-fig. 8*g*, *j*, *l*.
1979 *Adelograptus asiaticus* Mu; Wang *et al.*, pp. 499–500, pl. 1, figs 6 and 7; fig. 8*a*–*e*.
1979 *Adelograptus simplex* (Törnquist); Wang *et al.*, p. 501, fig. 9*a*.
1979 *Adelograptus victoriae* (T. S. Hall); Wang *et al.*, p. 501, fig. 9*b*.

Type specimen. Nat. Mus. Victoria No. P14240 (figured by Hall 1899, pl. 44, fig. 1) was designated lectotype by Berry (1966, p. 421). From the middle Lancefieldian (La2) near Lancefield, Victoria, Australia.

Diagnosis. Pendent or declined rhabdosome with many stipes increasing from 0·6–0·8 mm wide proximally to a maximum 1·2 mm. Autothecae with concave ventral margin, flared aperture and with bithecae, thecal density increasing from 8 in 10 mm proximally to 10 in 10 mm distally.

EXPLANATION OF PLATE 3

Figs 1 and 2. *Kiaerograptus undulatus* sp. nov. GSC 87436, MPS42C. 1, ×20, 2, ×40.

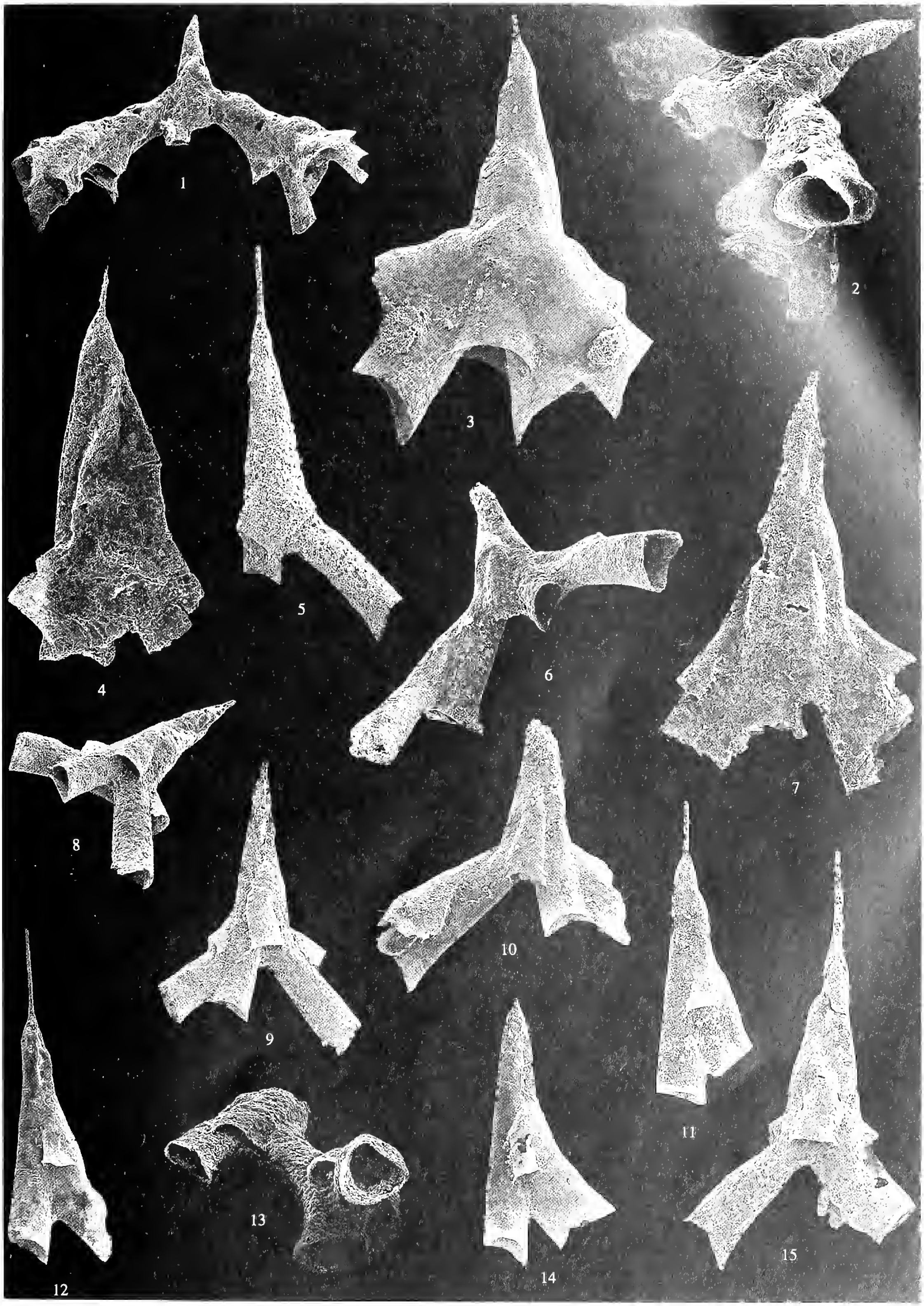
Figs 3, 4, 7. *Kiaerograptus magnus* sp. nov. 3, GSC 87433, SPI43. 4, GSC 87474, MPS42C. 7, GSC 87473, MPS42C. All ×40.

Figs 5, 6, 8–14. *Kiaerograptus bulmani* (Thomas, 1963). 5, GSC 87462, GP38. 6, GSC 87434, SPI43. 8 and 9, GSC 87459, GP38. 10, GSC 87442, SPI43. 11, GSC 87443, SPI43. 12, GSC 87446, SPI43 (also figured Text-fig. 5A, B). 13, GSC 87488, MPS42C. 14, GSC 87444, SPI43. All ×40.

Fig. 15. *Aorograptus victoriae* (T. S. Hall, 1899)?, GSC 87465, MPS42C, ×40.

Scanning electron micrographs of isolated specimens.

PLATE 3



WILLIAMS and STEVENS, *Kiaerograptus*, *Aorograptus*

Material and localities. Many isolated, three-dimensional and flattened, non-isolated specimens from all localities in the late Tremadoc of the Cow Head Group described in this paper.

Description. The rhabdosome has a pendent form with up to sixteen branches formed by four delayed dichotomies and sometimes exceeds 60 mm in diameter. Occasionally specimens are preserved flattened in horizontal orientation; in this instance the rhabdosome has a radiate, 'clonograptid' appearance. Stipe widths vary depending on astogeny, but are commonly 0·6–0·8 mm proximally, increasing distally to a maximum 1·2 mm.

The sicula is large, measuring 1·4–2·0 mm long; although such variation is not found in most other associated taxa, detailed observation has revealed continuous variation between the extremes and taxonomic division based solely on this criterion is therefore not warranted. The sicula is more or less straight, increasing gradually in diameter to 0·25–0·3 mm at the aperture. The nema is commonly preserved, reaching up to 4 mm long, and the rutellum is pronounced, extending 0·15 mm beyond the antirutellar margin.

Th1^1 buds from the prosicula, growing down in contact with the rutellar margin for 0·75 mm before bending out at an angle of 70° to the sicular axis. It subsequently curves down throughout its length, ending subparallel to the sicular axis after 0·8–1·2 mm. The aperture has a short selvage and is 0·3–0·4 mm wide (one half to two-thirds total stipe width). A sicular bitheca buds from the sicula 0·5 mm below the point of origin of th1^1. It varies tremendously in length, from little more than a concealed foramen to a theca with an aperture just above the point of divergence of the ventral wall of th1^1. The distal notch between the rutellar margin of the sicula and th1^1 is also rather variable in size, from 0·4–0·6 mm long.

Th1^2 buds from th1^1 not far below its point of origin, growing down and across the sicula at an angle of 20–30°. Development may be either dextral or sinistral. The ventral wall of th1^2 intersects the antirutellar margin of the sicular aperture, after which the theca arches gently down towards the thecal aperture, the free portion of ventral wall measuring 0·8–1·0 mm. Th1^2 is dicalycal, giving rise to both th2^1 and th2^2.

Th2^1 and th2^2 are also normally dicalycal, although one dichotomy is occasionally suppressed to give an asymmetrical branching pattern. Delayed but fairly regular dichotomous branching occurs throughout the rhabdosome, resulting in third or fourth order stipes in mature specimens. Each autotheca possesses a bitheca, whose apertures open on alternating sides of the stipe; these are also clearly visible at each dichotomy in isolated material. Such a pattern of thecae is strongly reminiscent of typical anisograptids, but careful examination has failed to reveal any hint of a stolon system embedded in the dorsal margin.

Thecal style is consistent throughout the rhabdosome, autothecae possessing concave ventral margins with flared apertures which occupy about one half total stipe width. Interthecal septae have an initial inclination of 10° to the dorsal margin, increasing ventrally to 20–30°. Thecal overlap is approximately one half total thecal length. Thecal density is unusual in that it increases from 8 in 10 mm proximally to 10 in 10 mm distally. It is unclear whether this is due to more steeply inclined thecae, shorter thecae, or greater thecal overlap, but is opposite to the situation found in most graptolites where thecal density decreases distally.

Remarks. All previously described specimens of *A. victoriae*, including the types, have been small rhabdosomes with only second order dichotomies. However, the lectotype has identical proximal dimensions and form and we have no hesitation in assigning our material to this species.

Bulman (1941) was the first to recognize that *A. clarki* was synonymous with *A. victoriae*. Berry (1966) subsequently considered the two to be distinct taxa, *A. clarki* being distinguished by lateral rather than dichotomous branching and less strongly declined stipes. Cooper (1979*a*) remarked that the two would probably prove conspecific; Cooper and Stewart (1979) formally synonymized them.

EXPLANATION OF PLATE 4

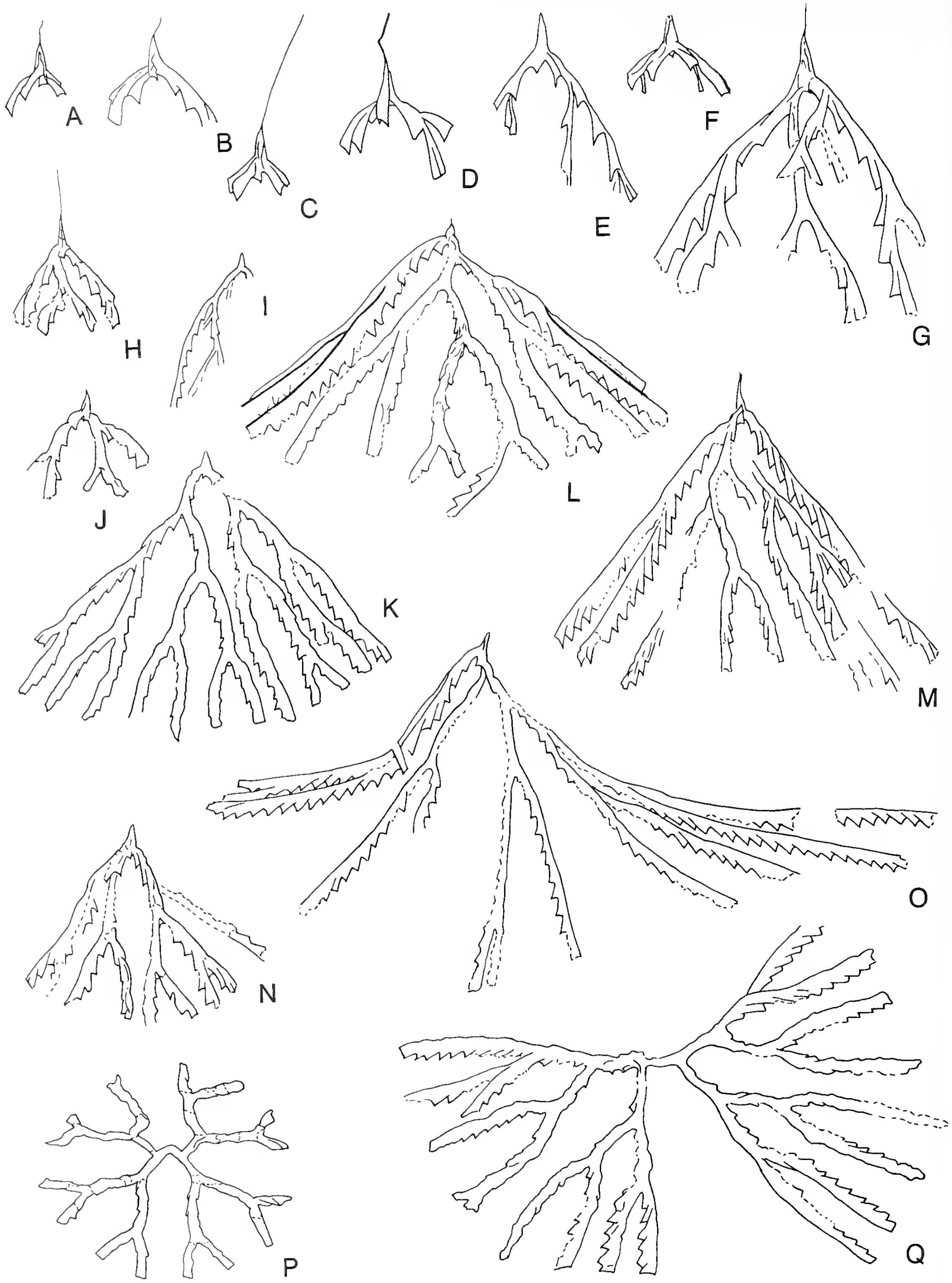
Figs 1–8. *Paratemnograptus isolatus* gen. et sp. nov. 1, GSC 87449, SPI43. 2, GSC 87450, SPI43. 3, GSC 87439, MPS42C. 4, GSC 87482, MPS42C. 5, GSC 87424, MPS42C. 6, GSC 87435, MPS42C. 7, GSC 87486, MPS42C. 8, GSC 87440, MPS42C. All ×40.

Figs 9–14. *Aorograptus victoriae* (T. S. Hall, 1899). 9 and 11, GSC 87437, MPS42C, ×20. 10, GSC 87418, note bitheca, MPS42C, ×20. 12, GSC 87422, MPS42C, ×20. 13, GSC 87477, MPS42C, ×40. 14, GSC 87425, MPS42C, ×40.

Scanning electron micrographs of isolated specimens.

PLATE 4

WILLIAMS and STEVENS, *Paratemnograptus*, *Aorograptus*



TEXT-FIG. 11. For legend see opposite.

We see no justification in retaining two separate species in the light of our own work and that of previous authors, and therefore follow Bulman (1941) and Cooper and Stewart (1979) in regarding *A. clarki* as a junior synonym of *A. victoriae*.

The species of '*Bryograptus*' figured by Hall (1914) and Bulman and Cooper (1969) is identical to our mature specimens of *A. victoriae*. Specimens assigned to '*B. pauxillus*, sp. nov.' (Benson 1933) and '*B. hunnebergensis* Moberg' (Benson and Keble 1936) were recognized by Bulman (1941, p. 115) as belonging to *A. victoriae*. The proximal ends of '*Bryograptus simplex* Törnquist' figured by Benson and Keble (1936) appear similar in branching pattern and overall form to *A. victoriae*, but the sicula is much longer (3 mm and 4·5 mm if their magnifications are correct). Törnquist's original specimens (1904, pp. 3–4, pl. 1, figs 1–4) have a similarly long sicula, but are recorded from the *T. phyllograptoides* Zone of southern Sweden. Williams and Stevens (1988*a*) considered this interval to be equivalent to the lower Arenig *T. akzharensis* Zone of the Cow Head Group. It is therefore most likely that *B. simplex* is synonymous with *Pendeograptus fruticosus* (J. Hall) or *P.* cf. *P. pendens* (Elles) as described by Williams and Stevens. The similarity of *A. victoriae* to the lower Arenig *P. fruticosus* is remarkable: proximal development, rhabdosome branching and thecal style (autothecae in *A. victoriae*) are all very similar, although the two may be distinguished by the longer sicula of *P. fruticosus* and bithecae and more numerous branching in *A. victoriae*.

The various Chinese and Russian species described by Mu (1955), Wang *et al.* (1979) and Tzaj (1968, 1974) all appear to be synonymous with *A. victoriae*, as do the specimens figured by Wang *et al.* (1979, fig. 9*a*) as *A. simplex* (Törnquist).

As noted in the discussion of *Aorograptus*, the original assignation of *A. victoriae* to *Bryograptus* is invalid following the definition given by Bulman (1970, p. V39), who stated that *Bryograptus* is an anisograptid which develops 'from three primary stipes by irregular and apparently lateral branching'. Obut's (1957) inclusion of both *Bryograptus* and the dichograptid genus *Pendeograptus* within a family Bryograptidae is therefore clearly unacceptable.

Genus ADELOGRAPTUS Bulman, 1941

Type species (by original designation). *Bryograptus*? *Hunnebergensis* Moberg, 1892, p. 92, pl. 2, figs 5–7 (?8 and 9).

Diagnosis. (revised using Bulman 1941, p. 114). Rhabdosome declined or horizontal, often somewhat lax and flexuous, formed from two primary branches by regular or irregular, commonly delayed, dichotomous branching. Sicular bitheca always present, additional bithecae and stolothecae present in some species, absent in others, autothecae straight, with simple apertures and low inclination, stipes consequently slender.

Remarks. The revision of *Adelograptus* permits incorporation of many slender, regularly branching taxa previously accommodated within the rather unsatisfactory genus *Clonograptus*. The type species of *Clonograptus* (*C. rigidus*) is now recognized as having a Lower Arenig age and probably belongs within the dichograptids (see previous discussion in text). Other more robust, pendent species originally assigned to *Bryograptus* (e.g. '*B.*' *victoriae*) but since transferred to *Adelograptus* (Bulman 1941) because of their two primary stipes are here assigned to a new genus *Aorograptus* (see generic remarks).

Although such a classification still has its limitations, it is closer to a true phylogenetic grouping

TEXT-FIG. 11. *Aorograptus victoriae* (T. S. Hall, 1899), A–G × 5, H–Q × 2·5. A, GSC 87374, GP38. B, GSC 87401, GP38. C, GSC 87405, GP38. D, GSC 87297, CHN8.32. E, GSC 87295, CHN8.34. F, GSC 87367, GP38. G, GSC 87397, GP38. H, GSC 87326, MPS42C. I, GSC 87379, GP38. J, GSC 87332, MPS42C. K, GSC 87310, MPS42C. L, GSC 87309, MPS42C (also figured Pl. 2, fig. 1). M, GSC 87355, MPS42C. N, GSC 87321, MPS42C. O, GSC 87320, MPS42C. P, GSC 87336, MPS42C. Q, GSC 87313, MPS42C.

than that used previously, all members having similar proximal developments and thecal styles. It permits the transfer of *Clonograptus tenellus* Linnarsson to *Adelograptus* as suggested by Maletz and Erdtmann (1987), making sense of Hutt's (1974) observation that *C. tenellus* and *A. hunnebergensis* have identical proximal development patterns and may only be distinguished following subsequent branching.

In his original diagnosis, Bulman (1941) stated that branching in *Adelograptus* was apparently lateral rather than dichotomous. All studies using isolated material of the genus since that time, including the present study and that of Hutt (1974), have found branching to be dichotomous; the diagnosis is therefore consequently emended.

The genus *Paradelograptus* was erected recently by Erdtmann *et al.* (1987) for non-bithecate forms which would previously have been assigned to *Adelograptus* or *Clonograptus*. The genus is characterized by slender thecae with simple or modified apertures, and considered to be ancestral to *Kinnegraptus* Skoglund, 1961 and other kinnegraptid genera. All their described species are from the lower Arenig and lack a sicular bitheca; none of our taxa may therefore be accommodated within this genus.

Adelograptus altus sp. nov.

Plate 5, figs 9–13; Plate 5, figs 14? and 15?; Text-fig. 12A–G

1979 *Adelograptus* sp.; Cooper and Stewart, text-fig. 7*d–f*, *h* (no description).

Derivation of name. From *altus* (Latin) meaning 'high', in reference to the relatively high level of divergence of the first two thecae from the sicula.

Type specimen. The holotype is GSC 87430, an isolated specimen mounted on an SEM stub, from MPS42C. Figured Plate 5, figure 12.

Diagnosis. Sicula 1·5–1·8 mm long with distal convex curvature, with both rutellar and antirutellar margins free distally. Sicular bitheca opens at same level where ventral wall of th1^1 diverges from sicula. Th1^1 and 1^2 are gently declined with concave free ventral margins and gently flared apertures, increasing from 0·2 mm diameter to 0·4–0·5 mm at the aperture.

Material and localities. Nine isolated, three-dimensional proximal fragments, eight flattened, non-isolated proximal fragments. Several possible mature, non-isolated rhabdosomes. From CHN8.30, SPI43, MPN17B, MPS42C.

Description. The species is defined primarily on its distinctive pattern of proximal development. Overall form is apparently similar to that of *A.* cf. *tenellus* (Moberg) with the exception of a slightly narrower funicle, but the two are clearly separated by the proximal form seen both in flattened and isolated material.

The sicula is 1·5–1·8 mm long measured along the rutellar margin, with a distal convex curvature. The sicular aperture is 0·2–0·25 mm wide, with a pronounced rutellum extending 0·05–0·1 mm beyond the antirutellar margin. Th1^1 buds from the prosicula on the rutellar side, growing down along this margin for 0·6–0·75 mm

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EXPLANATION OF PLATE 5

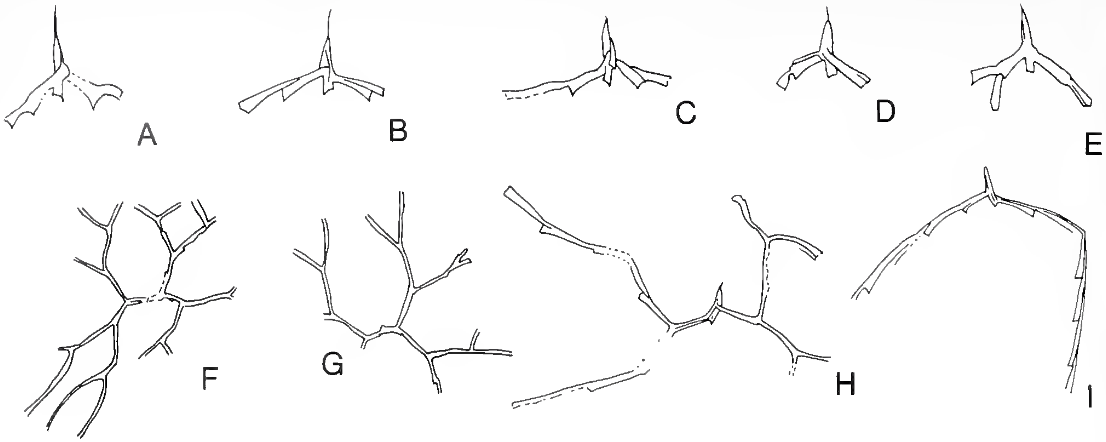
Figs 1–8. *Aorograptus victoriae* (T. S. Hall, 1899). 1, GSC 87421, MPS42C, ×40. 2, GSC 87457, MPS42C, ×40. 3, GSC 87426, MPS42C, ×40. 4, GSC 87475, ×40. 5, GSC 87472, MPS42C, ×20. 6, GSC 87453, MPS42C, ×40. 7, GSC 87478, MPS42C, ×20. 8, GSC 87487, MPS42C, ×20.

Figs 9–13. *Adelograptus altus* sp.nov. MPS42C, ×40 except Fig. 11 (= ×20). 9, GSC 87429. 10 and 11, GSC 87441. 12, GSC 87430, Holotype. 13, GSC 87455.

Figs 14 and 15. *Adelograptus altus* sp. nov.? Juvenile growth stages, ×40. 14, GSC 87460, GP38. 15, GSC 87427, MPS42C.

Scanning electron micrographs of isolated specimens.

WILLIAMS and STEVENS, *Aorograptus*, *Adelograptus*



TEXT-FIG. 12. A–G, *Adelograptus altus* sp. nov., A–E × 5, F and G, × 2·5. A, GSC 87302, MPN17B. B, GSC 87377, GP38. C, GSC 87360, MPS42C. D, GSC 87337, MPS42C. E, GSC 87341, MPS42C. F, GSC 87285, CHN8.30. G, GSC 87300, SPI43. H and I, *Adelograptus antiquus* (T. S. Hall, 1899)?, × 5. H, GSC 87340, MPS42C. I, GSC 87416, GP40.

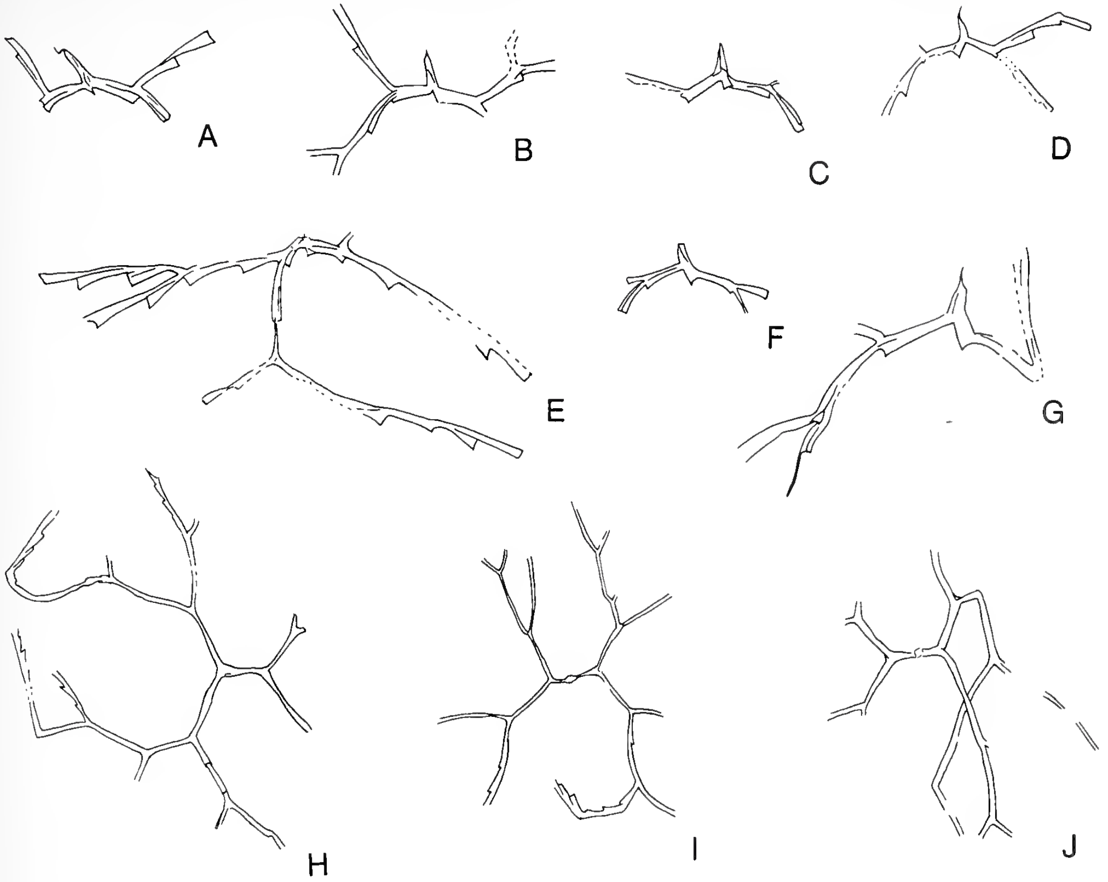
before turning sharply out, subtending an angle of 70–80° with the distal sicular axis. The rutellar wall of the sicula is free for 0·4–0·6 mm distally, while the sicular bitheca opens cryptically at the same level at which the ventral wall of th1^1 diverges from the sicula. The point of origin of the bitheca is unclear and appears to be concealed by the early dorsal wall of th1^1. The stipe is 0·15–0·2 mm wide where th1^1 leaves the sicula; the free ventral wall of th1^1 has as strong concave curvature, leading to a splayed-out aperture and an undeformed apertural stipe width of 0·4–0·5 mm. The ventral wall of th1^1 is free for 1·0–1·2 mm before the aperture is reached, which is 0·25–0·3 mm wide (i.e. two-thirds of total stipe width).

Th1^2 buds from th1^1 0·5 mm below its origin, growing immediately across and down the sicula at 45–50° from the sicular axis. Development may be either right- or left-handed; it is therefore meaningless to discuss reverse and obverse aspects of the sicula, as these vary from one specimen to the next. Once th1^2 has reached the antirutellar margin of the sicula it turns up slightly, subtending an angle of 30–40° with the distal sicular axis in most cases. It has a similar concave ventral margin and splayed-out aperture to th1^1, the stipe width measuring 0·2 mm initially, but increasing to 0·4–0·5 mm (undeformed) by the aperture.

The budding of th2^1 and 2^2 appears to be typically isograptid, with th1^2 dicalycal. There is no evidence for further dichotomies in isolated material, but one non-isolated specimen assigned to this species (Text-fig. 12E) and those of Cooper and Stewart (1979) show dichotomous branching of th2^1 and 2^2. Measurement of several slender 'clonograptid' rhabdosomes demonstrates several with funicles of equivalent width to that which would be expected from isolated specimens. We conclude that although branching is variable, mature rhabdosomes have overall appearances of those specimens illustrated in Text-figure 12F, G.

Remarks. The description of *A. altus* is based primarily on isolated, three-dimensional material, making comparison with other similar *Adelograptus* species difficult if known only from flattened, non-isolated specimens. The proximal budding pattern is similar to those shown by *A.* cf. *A. tenellus* and *Adelograptus* sp. A, but the sicula is longer than that of *A.* cf. *A. tenellus* and shorter than that of *Adelograptus* sp. A, while most specimens have a prominent 'notch' between the free ventral wall of th1^2 and the distal antirutellar margin of the sicula. Comparison using overlays clearly shows the incompatibility of the three species in terms of exact budding patterns and angles of thecal inclination.

The specimens figured by Cooper and Stewart (1979) as *Adelograptus* sp. are identical to those described here, with the exception of th1^1 which is marginally shorter. Unfortunately they did not describe their material or make any reference to it in the text. No other comparable specimens have been described or figured previously.



TEXT-FIG. 13. *Adelograptus* cf. *A. tenellus* (Linnarsson, 1871), A–F × 5, G × 10, H–J × 2·5. A, GSC 87403, GP38. B, GSC 87389, GP38. C, GSC 87409, GP38. D, GSC 87303, MPN17B. E, GSC 87347, MPS42C. F, GSC 87348, MPS42C G, GSC 87349, MPS42C. H, GSC 87398, GP38. I, GSC 87394, GP38. J, GSC 87395, GP38.

Adelograptus cf. *A. tenellus* (Linnarsson, 1871)

Plate 2, figs 2 and 3; Text-fig. 13A–J

cf. 1871 *Dichograptus tenellus*; Linnarsson, p. 795, pl. 16, figs 13–15.
cf. 1909 *Clonograptus tenellus* Linnarsson (and vars.); Westergård, pp. 68–72, pl. 4, figs 17–29.
cf. 1929 *Clonograptus tenellus* (Linnarsson); Stubblefield, pp. 278–262, text-figs 1, 8–11.
1936 *Bryograptus hunnebergensis* Moberg; Benson and Keble (*pars*), pp. 269–270, pl. 30, figs 14 and 15 (*non* pl. 30, figs 1–11 = *A. victoriae* (T. S. Hall)).
cf. 1987 *Adelograptus tenellus* (Linnarsson); Maletz and Erdtmann, pp. 180–182, pl. 1, figs *a–c*; pl. 2, figs *a–m*.

Material and localities. About ten flattened specimens from MPN17B, MPS42C and GP38 and five isolated, three-dimensional specimens from MPS42C.

Description. Rhabdosome with several slender stipes formed by delayed dichotomous branching from two primary stipes. The largest rhabdosome seen has a diameter of about 30 mm, with four dichotomies on the most complete portion, suggesting a total of thirty-two stipes. Dichotomous branching is apparently irregular, with a normal spacing of 3–5 mm (i.e. every two or three thecae). Thecal outline is rarely seen owing to preservation in scalariform view, but when present stipe width is seen to measure 0·35–0·4 mm proximally, increasing distally to a maximum 0·6 mm.

The sicula is 1·1–1·4 mm long, and has a gentle convex curvature with respect to the rutellar margin in the distal one-third to one half its length. It is 0·2–0·25 mm wide at the aperture, with a slight rutellum. $\mathrm{Th}1^1$ buds from the prosicula on the rutellar margin. It grows down in contact with this margin for 0·6–0·7 mm, before deflecting sharply out, subtending an angle of about 100° with the sicular axis. This leaves the distal rutellar margin of the sicula free for 0·4–0·5 mm. $\mathrm{Th}1^1$ then curves gently downwards until its aperture is reached, leaving a free ventral wall 1·0–1·1 mm long. The thecal aperture is 0·3 mm wide with a prominent flaring at the tip in some specimens. A sicular bitheca is present, originating a little below the point of origin of $\mathrm{th}1^1$ on the obverse side. The level of its aperture lies a little above the point of deflection of $\mathrm{th}1^1$, and is therefore not seen except in isolated specimens.

$\mathrm{Th}1^2$ buds high up from $\mathrm{th}1^1$, growing down and across the sicula on the reverse side, then curving out so that its ventral wall cuts the base of the antirutellar sicular margin. It subtends an angle of 60–70° with the sicular axis at its point of divergence; this angle is maintained for the remaining 1·0–1·1 mm of growth, although the theca sometimes curves down very slightly before the aperture. The funicle formed by the sicula and first two thecae measure 2·5–2·8 mm long when preserved horizontally to bedding.

$\mathrm{Th}2^1\mathrm{a}$ buds from $\mathrm{th}1^2$ on the rutellar margin of the reverse side some 0·7 mm above the base of the rutellum. It follows the dorsal wall of $\mathrm{th}1^1$ until just before the aperture is reached; at this point $\mathrm{th}2^1\mathrm{b}$ buds from $\mathrm{th}2^1\mathrm{a}$, the two growing in contact for about 0·15 mm before the aperture of $\mathrm{th}1^1$ is reached. They then diverge to give the first dichotomous branch. Although bithecae are apparently lacking on most thecae, branching fragments belonging to this or a related species show a bithecal aperture above the aperture of the autotheca when dichotomous branching occurs. Bithecae also occur at the dichotomies of several other unrelated late Tremadoc taxa, and are thought to represent an intermediate stage towards total loss of bithecae.

$\mathrm{Th}2^2\mathrm{a}$ buds from $\mathrm{th}1^2$ near its point of divergence from the sicula, developing and branching in a similar fashion to $\mathrm{th}2^1\mathrm{a}$. Each stipe then divides dichotomously every two to three thecae. Thecal density is a low, 6–7 in 10 mm where visible, although this is difficult to determine owing to frequent branching and usual preservation in scalariform view.

Remarks. Adelograptus tenellus was revised recently by Maletz and Erdtmann (1987), who selected a neotype and thoroughly discussed the morphological variation found within the species. They conclude the nominate species to be a lower Tremadoc form occurring definitely only in Scandinavia, the Baltic region and Britain. Records of the species from late Tremadoc strata are, therefore, likely to be erroneous. Our material differs from the type material in having a shorter funicle and noticeably lower thecal density. Variation is so great that definition of a new taxon is withheld pending further, more detailed quantitative studies of late Tremadoc material both from western Newfoundland and elsewhere.

A few previously published descriptions include material comparable to ours; some of Westergård's (1909) specimens of *C. tenellus* and varieties are very similar, but there is a great deal of variation in his figured specimens and probably more than one species represented. *C. tenellus kingi* Benson and Keble, 1936 is similar in overall form, but thecal density is extremely high (17–21 in 10 mm). Their specimen of '*C. tenellus*' (1936, pl. 32, fig. 4) also has a high thecal count. Benson and Keble (1936, pl. 30, figs 14 and 15) figured two proximal fragments more-or-less identical to our material; these are referred to *Bryograptus simplex* Törnquist in the plate description, as are figs 12 and 13. The latter two specimens have a very different appearance, are referred to '*B. hunnebergensis*' in the text, and probably belong to *A. victoriae* (see discussion of *A. victoriae* elsewhere in this paper).

The Newfoundland specimens of *A.* cf. *tenellus* have a wider funicle than '*C. tenellus sensu lato*' of Cooper (1979*b*, fig. 5*c*) and Cooper and Stewart (1979, fig. 8*m*); both these appear to be a different species.

Adelograptus antiquus (T. S. Hall, 1899)?

Text-fig. 12H, I

?1899 *Leptograptus antiquus*, n. sp.; T. S. Hall, p. 166, pl. 17, figs 5 and 6.
?1979*a* *Adelograptus*? *antiquus* (T. S. Hall); Cooper, pp. 51–54, pl. 2, fig. *c–e*; fig. 17*a–k*, 18.
?1979 *Kiaerograptus antiquus* (T. S. Hall); Cooper and Stewart, pp. 791–792, text-fig. 8*d*, *e*. (summary only)

Material and localities. Two flattened specimens from MPS42C and GP40.

Remarks. Careful comparison of these two specimens with *Adelograptus* species from western Newfoundland reveals them to differ in terms of their small, slender sicula, wide funicle and low thecal density. These however appear to agree with those given for *A. antiquus* by Cooper (1979*a*) in his detailed revision of the species, but are insufficient for certain identification. Their slender, widely spaced proximal region is reminiscent more of *Adelograptus* than *Kiaerograptus*, which is why we return the species to the former genus as assigned questionably by Cooper (1979*a*).

Adelograptus sp. A

Plate 6, figs 1–5; Text-fig. 14H, J

Material and localities. Three flattened, non-isolated specimens from MPN17B, MPS42C and GP40. Nine three-dimensional, isolated specimens from MPS42C.

Description. This species is known only from isolated and non-isolated proximal fragments; overall form of the rhabdosome is consequently uncertain.

The most distinctive feature is the long, thin sicula, which is commonly 1·5 mm long. It is straight throughout the first two-thirds of its length, but displays a gentle, distal convex curvature with respect to the rutellar margin. The rutellum is pronounced, extending 0·15–0·2 mm beyond the antirutellar margin.

Th1^1 buds from the prosicula, growing down along the rutellar margin for 0·6–0·8 mm before bending out sharply, subtending an angle of 60–70° with the sicular axis and leaving the rutellar margin free for 0·5–0·6 mm. A prominent sicular bitheca buds from the sicula about half way down the metasicula on the reverse side. It has a prominent aperture lying between the rutellar margin of the sicula and ventral wall of th1^1, a little below the point where the ventral wall of th1^1 leaves the sicular margin. Th1^1 is 0·2 mm wide at the point where it diverges from the sicula. Its free ventral wall is 0·9–1·1 mm long and almost straight, but flares towards the aperture which measures 0·4 mm wide (one half total stipe width).

Th1^2 buds from th1^1 on the obverse side just above its point of deflection. It grows down and across the sicula, the ventral wall diverging from the antirutellar margin a little above the sicular aperture. This occasionally results in a slight 'notch' at the base of the antirutellar wall. Th1^2 grows down at 40–50° from the distal sicular axis; it is almost straight but flares slightly towards the aperture. The free ventral wall is 0·7–0·8 mm (i.e. less than that of th1^1), while thecal widths are similar.

Development of th2^1 and th2^2 is as found for other associated taxa; one or both are sometimes dichotomous, or dichotomies may be delayed by one or more thecae. As stated above, overall form of the rhabdosome is uncertain.

Remarks. This species may be distinguished from other coexisting taxa by its long, slender sicula and levels of divergence of th1^1 and th1^2 from the sicula. Dichotomous branching is irregular and may be delayed or consecutive. As the overall form of the rhabdosome is uncertain and only limited material is available, it would be unwise to formally erect a new species at the present time.

No previously described taxa of similar type have a sicula approaching this size. From the few larger fragments found, overall style of branching appears to be most similar to the irregular form of *Adelograptus antiquus* (T. S. Hall).

Adelograptus filiformis sp. nov.

Text-fig. 14A–G

?1936 *Bryograptus* (?) *antiquus* var. *inusitatus* var. nov.; Benson and Keble, pp. 267–268, pl. 30, figs 17 and 18.

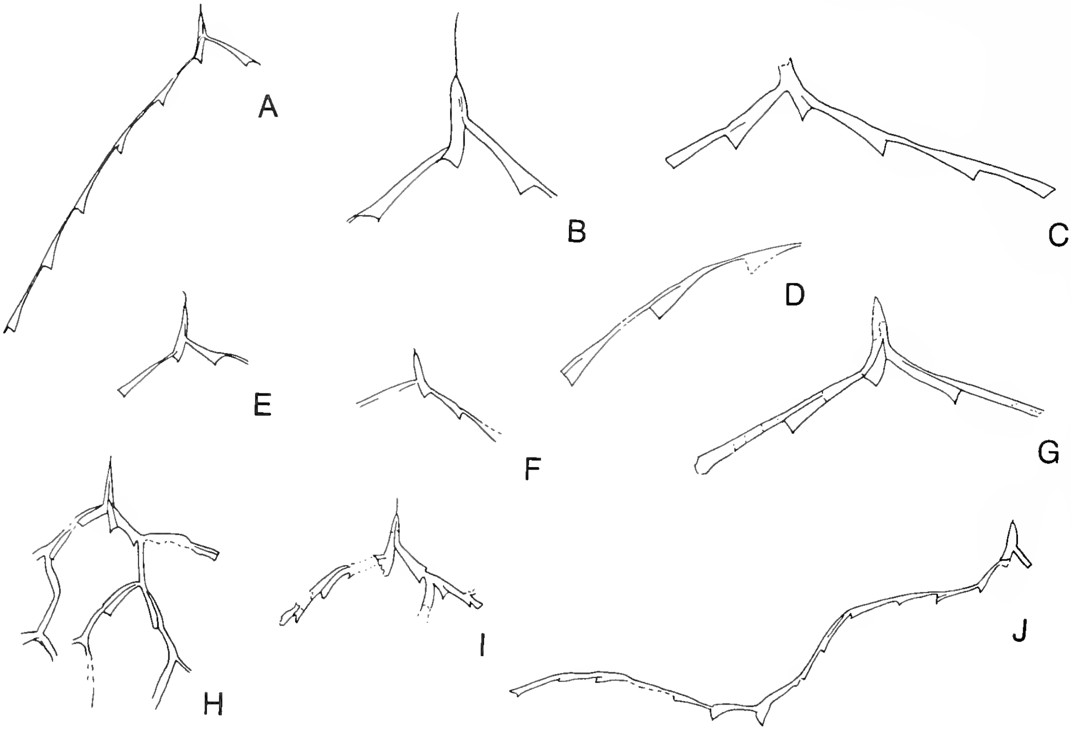
1974 *Kiaerograptus*(?) cf. *pritchardi* (T. S. Hall); Jackson, p. 51, pl. 5, fig. 3; text-fig. 2*a*, *c*, *d*.

?1982 *Kiaerograptus antiquus* (T. S. Hall); Gutierrcz Marco, fig. 2*a*–*e*.

Derivation of name. From *filum* (Latin), meaning thread-like, in reference to the extremely slender stipes.

Type specimen. The holotype is GSC 87391, figured Text-figure 14A. From GP38.

Diagnosis. Extremely slender, biramous, declined to pendent rhabdosome, stipes measuring



TEXT-FIG. 14. A–G, *Adelograptus filiformis* sp. nov. A, GSC 87391, Holotype, GP38, ×5. B, GSC 87387, GP38, ×10. C, GSC 87350, MPS42C, ×10. D, GSC 87298, CHN8.32, ×10. E, GSC 87299, SPI43, ×5. F, GSC 87304, MPN17B, ×5. G, GSC 87305, MPN17B, ×10. H–J, *Adelograptus* sp. A, ×5. H, GSC 87417, GP40. I, GSC 87306, MPN17B. J, GSC 87312, MPS42C

EXPLANATION OF PLATE 6

Figs 1–5. *Adelograptus* sp. A. MPS42C, ×40. 1, GSC 87469. 2, GSC 87431. 3, GSC 87484. 4 and 5, GSC 87468.

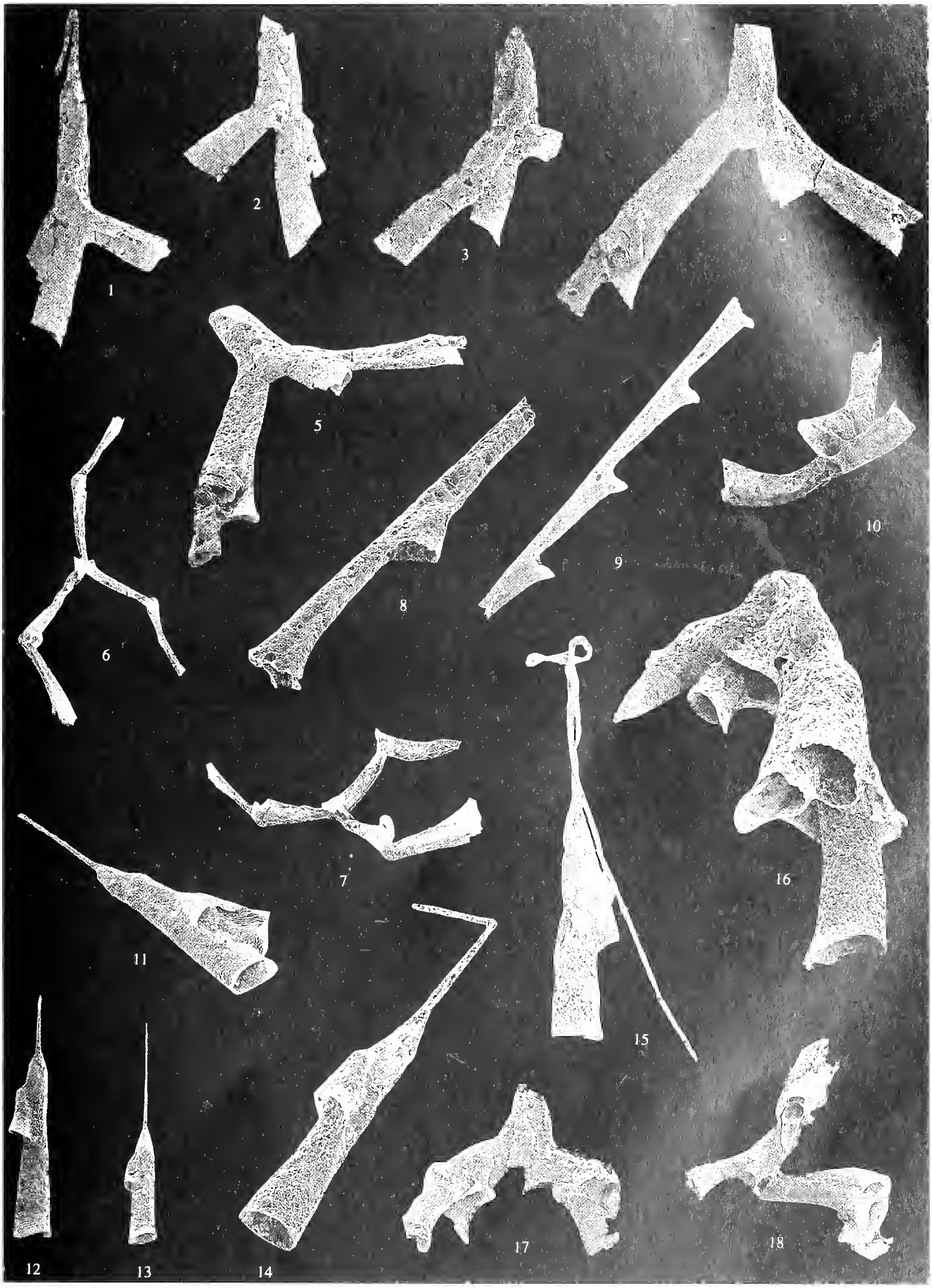
Figs 6–10. Stipe fragments and branches from indet. *Adelograptus*. MPS42C. 6 and 7, GSC 87438, ×20. 8, GSC 87432, ×40. 9, GSC 87466, ×20. 10, GSC 87485, ×40.

Figs 11–15. Indet. juvenile growth stages. 11, GSC 87445, SPI43, ×40. 12, GSC 87489, SPI43, ×40. 13, GSC 87447, SPI43, ×40. 14, GSC 87463, GP38, ×80. 15, GSC 87461, GP38, ×80.

Figs 16–18. *Clonograptus* sp. B. 16, GSC 87458, MPS42C, ×40. 17, GSC 87428, MPS42C, ×20. 18, GSC 87467, MPS42C, ×20.

Scanning electron micrographs of isolated specimens.

PLATE 6



WILLIAMS and STEVENS, *Adelograptus*, *Clonograptus*

0·2–0·3 mm at thecal apertures, but only 0·08–0·1 mm directly after apertures. Sicula with bitheca, other bithecae apparently lacking. Th1^1 with high divergence, leaving 0·5–0·6 mm of distal sicula wall free. Thecal density 6–6·5 in 10 mm.

Material and localities. Two probable isolated fragments from MPS42C. Eleven non-isolated, flattened specimens from CHN8.32; SPI43; MPN17B, MPS42C; GP38.

Description. The rhabdosome consists of two extremely slender, gently declined stipes. The longest stipes fragment present in the material from western Newfoundland is only 10 mm long; one of the specimens figured by Jackson (1974, text-fig. 2*d*) however had stipe about 18 mm long with strong convex curvature, such that distally the stipes pointed inwards. Stipe width at the initial free part of each theca is a uniform 0·08–0·1 mm, increasing to 0·2–0·3 at the aperture.

The sicula is 1·2–1·4 mm long, with an apertural width of 0·2–0·25 mm. It is inclined with respect to the stipes, has a strong convex curvature with respect to the rutellar margin and a pronounced rutellum. Proximal development is unclear; th1^1 buds from the prosicula and grows down in contact with the rutellar wall of the sicula for only about 0·5 mm before diverging sharply out, subtending an angle of 60–70° with the sicular axis. The distal rutellar margin of the sicula is left free for 0·5–0·6 mm (rarely 0·4 mm). The dorsal thecal margin remains straight, but the ventral wall curves gently down towards the aperture, such that inclination of the ventral wall with the dorsal stipe margin increases from about 0° proximally to 30° at the level of the aperture. The free portion of th1^1 is of variable length, measuring 1·2–1·5 mm (cf. Jackson 1974, whose specimens had an extremely short free portion of 0·5–0·8 mm). The aperture of th1^1 and remaining thecae occupies two thirds of total stipe width. Although no hint of a sicular bitheca has been seen in any flattened, non-isolated specimens, the isolated material clearly shows a small bithecal aperture in the notch left by the divergence of th1^1 from the rutellar wall of the sicula.

Th1^2 apparently buds from th1^1 at its point of deflection. Initially it grows across and slightly down, then runs in contact with the antirutellar margin of the sicula until the sicular aperture is reached. It subsequently turns out at an angle of 20–30° from the distal sicular axis. The free ventral wall of th1^1 part of th1^2 and that of all subsequent thecae behave as th1^1. The origin of th2^1 is unclear; if development is similar to other species from this assemblage, it would bud from th1^2. In this instance, it must have an extremely slender protheca less than 0·05 mm wide. With the exception of the sicular bitheca, there appears to be no other bithecae in the rhabdosome, neither does there appear to be any branching. Thecal density is exceptionally low throughout the rhabdosome, at a constant 6–6·5 in 10 mm.

Remarks. The only previous certain record of this distinctive but elusive species was by Jackson (1974), who referred it to *K.*? cf. *pritchardi.* His specimens from the Yukon, northern Canada are very similar but differ in the shorter free portion of th1^2 (0·5–0·8 mm as opposed to 1·2–1·5 mm). The free portion of th1^2 is, however, comparable in length to that of our specimens (1·3–1·7 mm as opposed to 1·2–1·4 mm), as is thecal density and stipe width. Judging from his illustrated examples, it appears that such variation may have been due to tectonic stretching (note particularly his text-fig. 2*d*).

Although several other slender taxa found within this stratigraphical interval are similar in appearance, *K. filiformis* may be reliably distinguished from them all by its high divergence of th1^1 from the sicula, extremely narrow stipes in the portion immediately following the apertures, and low thecal density. As recorded by Jackson (1974), no specimen seems to have possessed more than two stipes.

Cooper (1979*a*) expanded the definition of *Adelograptus antiquus* (T. S. Hall) to include a variety of forms with siculae and first two thecae of varying dimensions and emphasizing the symmetry of the proximal end. We accept this revision, but our specimens fall well outside his described population with a consistently longer and more slender sicula and longer first two thecae. Thecal spacing is also lower at 6–6·5 in 10 mm instead of 7 in 10 mm. Some of Cooper's end members (e.g. Cooper 1979*a*, fig. 17*h*) approach *A. filiformis*, but are still noticeably different. Cooper (1979*a*) included *K.*? cf. *pritchardi* of Jackson (1974) and *B.*? *antiquus inusitatus* Benson and Keble, 1936 with *A. antiquus*. Although they appear to be tectonically deformed, in our opinion Jackson's specimens seem closer to *A. filiformis* than to *A. antiquus*, with the exception of a short th1^1.

Although Jackson (1974) recorded thecal density as 9–10 in 10 mm, this varies from 7–10 in 10 mm in his figured specimens, depending on orientation to stretching direction. Cooper (1979*a*, p. 53) pointed out that Benson and Keble's figured specimen of *B.*? *antiquus inusitatus* differed from their written description, notably by having wider thecal spacing (3–3·5 instead of 6–7 in 10 mm). This would seem to be caused by an error in scale of illustration (probably × 4 rather than × 2), but as their types have not been located (Cooper, 1979*a*, p. 33), this is impossible to ratify, neither is the affinity of *B.*? *antiquus inusitatus* with either *A. antiquus* or *A. filiformis*.

Genus CLONOGRAPTUS Nicholson, 1873

Type species. Graptolithus rigidus J. Hall, 1858, p. 146. Subsequently designated by Miller (1889, p. 179).

Remarks. Clonograptus has been considered a typically 'dendroid' genus (in the traditional sense: cf. Fortey and Cooper 1986) by most authors since its original designation, although the dichograptid appearance of its autothecae and apparent lack of bithecae or stolon system has been noted by several workers (e.g. Jackson 1973; Braithwaite 1976). Recognizing this, Maletz and Erdtmann (1987, p. 180) included *Clonograptus* within the Dichograptidae rather than the Anisograptidae, and transferred many taxa previously included within the genus to *Adelograptus*.

We consider the type species of *Clonograptus* to be synonymous with one of Hall's other species, '*Graptolithus*' (usually referred to *Clonograptus*) *flexilis*, first described in the same publication as *C. rigidus* on the preceding page (J. Hall 1858, pp. 145–146). It could be argued that *C. rigidus* is therefore a junior synonym of *C. flexilis*, but we consider it best to retain *C. rigidus* as the species name in the cause of nomenclatorial stability.

Restudy of Hall's type material from Levis, Quebec by one of us (S.H.W.), revealed the types of both species to originate from the lower Arenig of that locality, an interval equivalent to the *T. akzharensis* Zone of western Newfoundland (Williams and Stevens 1988). This zone separates the *T. approximatus* Zone from the overlying *P. fruticosus* Zone. In both regions, diverse assemblages of both dichograptids (e.g. *Tetragraptus*, *Didymograptus* (*Expansograptus*), *Pendeograptus*, *Pseudophyllograptus*) and traditional 'dendroid' taxa (e.g. *Rhabdinopora*, *Dendrograptus*, *Arcanthograptus*) are present. Although three-dimensional, isolated material was not recovered from this interval, the representatives of *Clonograptus* do indeed appear to bear more resemblance to the dichograptids than to the anisograptids, and we tend to agree with the conclusions of Maletz and Erdtmann (1987). Erdtmann *et al.* (1987, p. 123) transferred *Clonograptus smithi* Harris and Thomas, 1938 to their new kinnegraptid genus *Paradelograptus*. *C. smithi* is, however, from the lower Bendigonian (equivalent to the *T. approximatus* or *T. akzharensis* zones) and appears very similar to *C. rigidus*/*C. flexilis*.

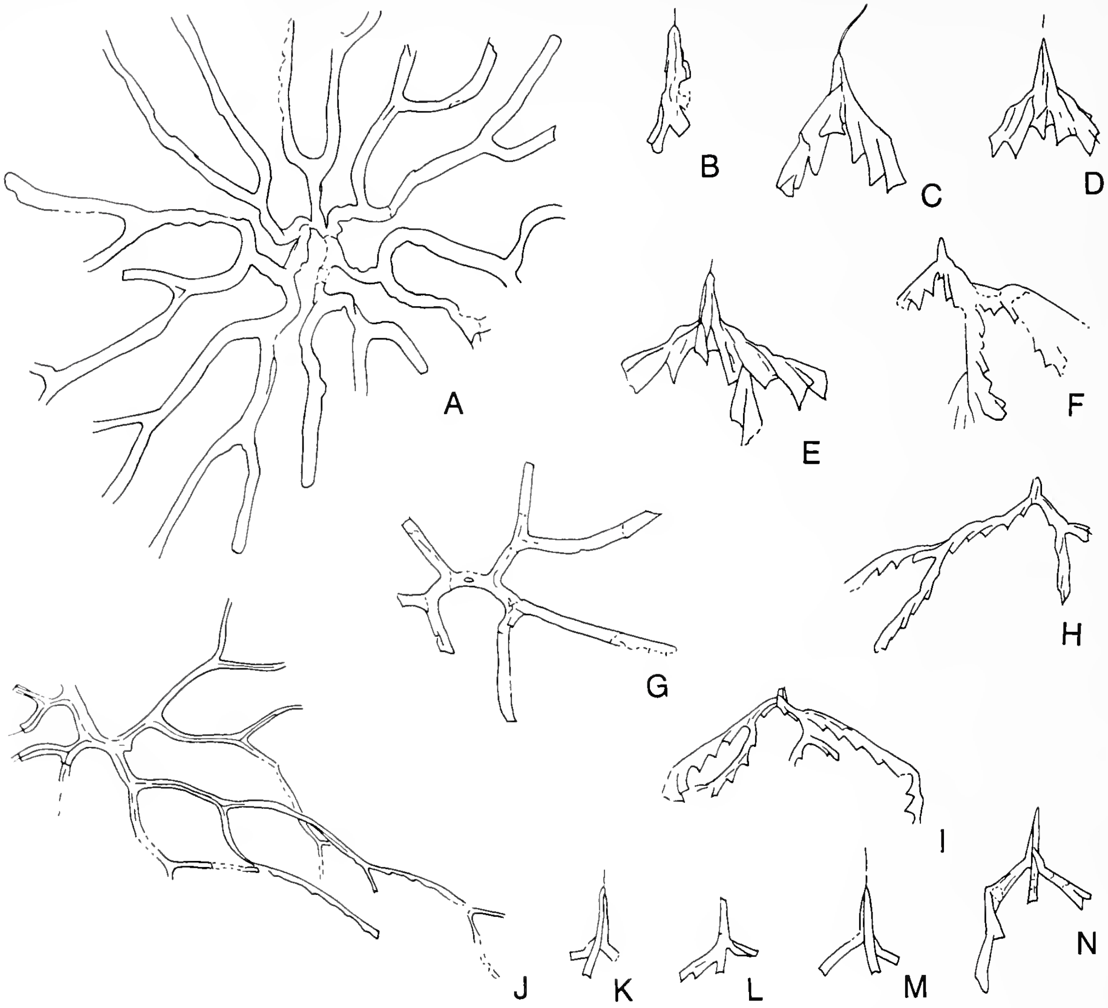
If typical *Clonograptus* belongs to the Dichograptidae, it is unlikely that taxa from the lower, middle or even upper Tremadoc should be assigned to the genus if the presence of bithecae or a stolon system is considered of taxonomic significance at the generic level. Final revision of the generic definition should, however, be withheld until isolated material of '*Clonograptus*' has been recovered from both the Tremadoc and lower Arenig. We therefore here refer our late Tremadoc '*Clonograptus*-like' taxa to '*Clonograptus*?'

Clonograptus? sp. A.

Plate 2, fig. 6; Plate 6, figs 16–18; Plate 7, figs 1–5; Text-fig. 15A–F

Material. Several flattened specimens from CHN8.32, MPS42C and GP38. Ten isolated, three-dimensional specimens from MPS42C.

Description. The rhabdosome reaches over 30 mm in diameter, somewhat irregular, delayed dichotomous branching producing up to at least thirty-two stipes distally from the two primary stipes. The proximal region



TEXT-FIG. 15. A–F, *Clonograptus* sp. A, A and F ×2·5, B–E ×5. A, GSC 87418, GP40. B, GSC 87342, MPS42C. C, GSC 87343, MPS42C. D, GSC 87373, GP38. E, GSC 87380, GP38. F, GSC 87344, MPS42C. G–I, *Clonograptus* sp. C, ×2·5. G, GSC 87351, MPS42C. H, GSC 87346, MPS42C. I, GSC 87419, GP40. J, *Clonograptus* sp. B, GSC 87314, MPS42C, ×2·5 (also figured Pl. 2, fig. 5). K–N, *Rhabdinopora* sp., MPS42C, ×5. K, GSC 87338. L, GSC 87345. M, GSC 87352. N, GSC 87353.

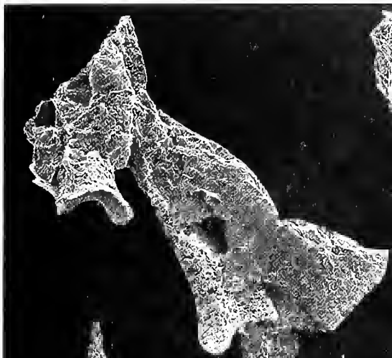
EXPLANATION OF PLATE 7

Figs 1–5. *Clonograptus* sp. A. MPS42C, all ×40 except Fig. 3 (= ×20). 1, GSC 87479. 2, GSC 87481. 3, GSC 87423. 4, GSC 87470. 5, GSC 87476.

Figs 6–12. *Rhabdinopora* sp. 6, GSC 87451, SPI43. 7, GSC 87456, MPS42C. 8, GSC 87483, MPS42C. 9, GSC 87452, SPI43. 10, GSC 87419, MPS42C. 11, GSC 87454, MPS42C. 12, GSC 87420, MPS42C. All ×40, except fig. 6 (= ×80).

Figs 13–17. Indet. dendroid distal fragments. 13, GSC 87448, SPI43. 14 and 15, GSC 87464, GP38. 15, GSC 87471, MPS42C. 17, GC 87480, MPS42C. All ×40 except fig. 17 (×80).

Scanning electron micrographs of isolated specimens.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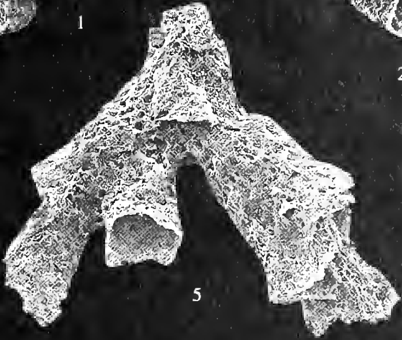
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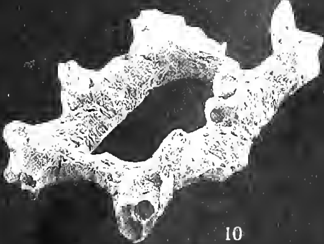
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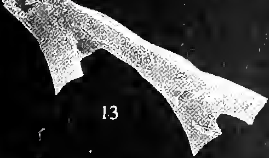
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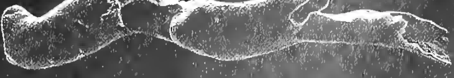
17

WILLIAMS and STEVENS, *Clonograptus*, *Rhabdinopora* is generally preserved in scalariform view, with stipe widths of about 0·7 mm; distal stipe widths are similar, both in scalariform and lateral aspect. The stipes have an irregular appearance owing to the presence of bithecae throughout the rhabdosome. Dichotomous branching occurs throughout the rhabdosome at intervals of 2–8 mm; failed dichotomies commonly result in asymmetrical rhabdosomes.

The sicula is about 2 mm long, with a distinctive concave apertural outline formed by a prominent rutellum and slight antirutellar process. Proximal development has not been observed clearly, but appears to be similar to most coeval graptolites, with a prominent sicular bitheca opening at the level of divergence of the ventral wall of th1^1 from the rutellar margin. Th1^1 and 1^2 are strongly declined, giving a narrow, pendent appearance to the proximal region. Their free ventral margins are gently concave and are 1·8–2·0 mm long. The funicle is normally deformed due to flattening of the rhabdosome in a plane perpendicular to that of the sicula, th1^1 and 1^2. Both th1^2 and 2^1 dichotomise, as do many subsequent thecae, giving rise to the multi-stiped rhabdosome.

All autothecae apparently possess bithecae, opening on alternate sides of the stipes. The ventral margins of autothecae display gentle concave curvature, have simple apertures occupying one half to one third total stipe width and have an almost uniform spacing of ten in 10 mm throughout the rhabdosome.

Remarks. This species appears to differ from all described previously, but inadequate material exists to justify formal erection of a new taxon. The overall appearance of the rhabdosome and thecal style is reminiscent of *Clonograptus kingi* Benson and Keble, 1935. Their species is, however, minute, with slender stipes 0·2 mm wide and a very high thecal density.

Both proximal and distal isolated fragments are extremely distinctive, owing to their robust form, ubiquitous bithecae, and curved autothecae. Although very different in proximal appearance and thecal style, it is sometimes difficult to distinguish poorly preserved specimens from *Aorograptus victoriae* preserved in dorsal view. The latter species possesses more simple autothecae, only has bithecae at dichotomies, and the proximal region has a very different appearance.

Clonograptus? sp. B.

Plate 2, fig. 5; Text-fig. 15J

Material. Two flattened specimens from MPS42C and GP38.

Remarks. These two specimens are preserved in scalariform orientation, and characterized by heavy cortical thickening in the proximal region. This reduces distally, resulting in narrowing stipes. Details of lateral stipe width, thecal style, etc., have not been observed due to both orientation of the rhabdosome and to the cortical thickening.

Examples of '*Clonograptus*' with similar appearance have been recorded several times before, both from the top Tremadoc and other stratigraphic levels. The specimen figured by T. S. Hall (1914, pl. 8, fig. 3) as '*C. tenellus callavei* Lapworth' and refigured by Bulman and Cooper (1969, fig. 5*f*) is probably identical. Our specimens are also similar in appearance to J. Hall's (1858) type specimens of *C. rigidus* and *C. flexilis* regarding their distinctive cortical thickening, but his material from the lower Arenig of Quebec reaches much greater dimensions and critical comparison is not possible. If the specimens from western Newfoundland are indeed similar to Hall's types, it demonstrates that they may be assigned unequivocally to *Clonograptus s.s.*

Clonograptus? sp. C

Text-fig. 15G–I

Material. Several flattened, fragmentary specimens from MPS42C and GP40.

Remarks. These specimens are characterised by a funicle of varying width due to irregular, commonly delayed, first dichotomous branching, relatively slender stipes 0·8 mm wide, and simple autothecae numbering about eight in 10 mm. The proximal region is gently declined and open, in contrast with *Clonograptus*? sp. A. No isolated material or well preserved flattened specimens have been recovered exhibiting complete proximal development; it is possible that *Clonograptus*? sp. C is closer to *Aorograptus victoriae* than to *Clonograptus*, but the lack of flared apertures and overall appearance of the proximal region appear to be different from that genus.

Genus RHABDINOPORA Eichwald, 1855

Type species. Gorgonia flabelliformis Eichwald, 1840, p. 207. By subsequent designation of Erdtmann (1982)

Diagnosis. Rhabdosome conical (juvenile stages may possess reduced conicality), coni-siculate throughout all developmental stages, with or without proximal buoyancy structures; branching dichotomous, diverging from tricalycal or quadricalycal initial stolonal budding; stipes straight, subparallel to parallel, connected by transverse dissepiments, anastomosis rare; autothecae denticulate, commonly spined, bithecae normally inconspicuous (from Erdtmann 1982, pp. 128–129).

Remarks. Erdtmann's revision of *Dictyonema* and *Rhabdinopora*, restricting the former genus to rooted species, is here accepted. Our planktonic forms are therefore assigned to *Rhabdinopora*, although previously they would have been considered 'typical' *Dictyonema*.

Rhabdinopora sp.

Plate 2, figs 7–11, 13; Plate 7, figs 6–12; Text-fig. 15K–N

Material. Many three-dimensional, isolated fragments from SPI43 and MPS42C, and flattened specimens from all late Tremadoc localities in the Cow Head Group.

Remarks. The genus *Rhabdinopora* is currently under revision by Erdtmann and others. Characters of taxonomic importance are still uncertain, and we withhold full taxonomic treatment pending further revision of the genus. Three primary stipes are clearly visible in isolated material, and the slender sicula and proximal development are readily identifiable in flattened specimens. A 'flotation sac' is present on one of the specimens, while thecal style, dissepiments and net-like, parabolic rhabdosome are all characteristic of *Rhabdinopora*.

This ubiquitous form continues into the lower Arenig, where it is common in both the *T. approximatus* and *T. akzharensis* zones, but rare after that level. The disappearance of *Rhabdinopora* from the sections may be stratigraphically controlled, but in our opinion is more likely related to subtle changes in paleoecology.

miscellaneous indet. Graptoloids

Plate 2, fig. 12; Plate 7, figs 13–17

Remarks. A variety of distal stipe fragments are present in the late Tremadoc, flattened in the shale and as three-dimensional isolated fragments from dissolved limestone. They are not identifiable without additional, more complete material, but due to their distinctive nature a selection is here figured for completeness.

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MIDDLE TRIASSIC HOLOTHURIANS FROM NORTHERN SPAIN

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ABSTRACT. An abundant fauna of well-preserved holothurians is described from the Middle Triassic (Ladinian) of Collbató, northern Spain. Three new genera and species are represented, *Strobilothyone rogenti*, a heterothyonid, *Monilipsolus mirabilis*, a psolid, and *Collbatothuria danieli* an aspidochirote of uncertain familial affinities. A new subfamily, Monilipsolinae, is created for *Monilipsolus*. Holothurians had clearly achieved considerable diversity by the Middle Triassic; at least four of the six currently recognized orders were established by this time. Holothurians were also ecologically diverse by the Middle Triassic with epibenthic, deposit-feeding species, infaunal, suspension-feeding species and epifaunal, attached, suspension-feeding species all represented.

OF the five classes of echinoderm alive today, none has a poorer fossil record than the holothurians. There are some 1160 named species alive today (Pawson 1982), and these are found in virtually all marine habitats. Yet only a handful of complete specimens of fossil holothurians have ever been discovered. This is partially explained by the relatively low fossilization potential of holothurians, since the great majority have their skeleton reduced to microscopic spicules. However, the holothurian fossil record is considerably worse than might be expected. For example, although several families of dendrochirotids possess an imbricate skeleton of large calcite plates and might be expected to be preserved in Konservat Lagerstätten, none has ever been reported as fossils. Complete fossil holothurians have been reported from just six localities:

1. Hunsrückschiefer, Lower Devonian of Budenbach, West Germany. This has yielded seven specimens of *Palaeocucumaria hunsrueckiana* Lehmann, described by Seilacher (1961).
2. Francis Creek Shale, Middle Pennsylvanian of Illinois, USA. Over two thousand specimens of an *Achistrum* sp., only a preliminary description of which has so far been published (Sroka 1988).
3. Muschelkalk, Middle Triassic, of Tarragona, Spain. One specimen each of the elasipod *Oneirophantites tarragonensis* Cherbonnier and the aspidochirote *Bathysynactites viai* Cherbonnier, preserved as impressions in calcareous silts (Cherbonnier 1978).
4. Upper Hauptrogenstein, Upper Bajocian, Middle Jurassic of Schinznach, Switzerland. A single specimen of the stichopid *Holothuriopsis pawsoni* Hess (Hess 1973) which preserves body wall spiculation but little else.
5. Solenhofen Limestone, Kimmeridgian, Upper Jurassic of Solenhofen, West Germany. Two species have been identified as holothurians, *Proholothuria armata* Giebel and *Pseudocaudina brachyura* Broili, the latter based on a single specimen (Frizell and Exline 1966). *P. armata* is a worm-shaped fossil that shows no details and is indeterminate to phylum. *P. brachyura* shows longitudinal banding and might be a holothurian, though Hess (1973) has questioned this.
6. Lower Cretaceous (Albian) of Tepexi de Rodriguez, Puebla, Mexico. A complete holothurian is recorded from here (Seibertz 1988), but no description of this has yet been published.

The lack of complete specimens creates major problems in investigating the evolutionary history of holothurians. Holothurian spicules are relatively common as microfossils and a parataxonomy has been established on spicule morphology alone (e.g. Frizell and Exline 1955, Deflandre-Rigaud 1962). However, this may bear little correlation with natural biological groupings and it is difficult to deduce much about the mode of life of extinct holothurians from spicule morphology. Further problems arise because higher taxa of holothurians are defined to a large degree on soft tissue

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anatomy, such as the shape of the feeding tentacles or the arrangement of gonads, characters that are unknown even in those few fossil species preserved as complete specimens. Complete fossil holothurians can, however, generally be placed within a biological classification and provide direct information about the ecological diversification of the group.

The discovery of a new assemblage of well-preserved fossil holothurians belonging to three families from the Middle Triassic of Catalonia, north-east Spain is thus totally unexpected. The locality was discovered in 1986 when David Brusi, a lecturer at the Teacher's College of the Universidad Autónoma de Barcelona, collected two ophiuroids from a disused limestone quarry at Pedrera d'en Rogent. These specimens were shown to one of us (J. G.) who later visited the locality with Brusi. On this trip several fossil holothurians were found and photographed but not collected because it was felt that this was a difficult operation and required a portable rock-saw. A second visit by J. G. was made in November 1987, equipped with power tools, and many fossil holothurians were collected together with other fossils. Just prior to this second visit a number of specimens had been collected from this quarry by an amateur palaeontologist, Dr Daniel Gutiérrez. The ophiuroids collected by him were later described (Calzada and Gutiérrez 1988) but the holothurians were given to us for study. A preliminary account of this holothurian fauna was presented at the Fourth Annual Meeting of the Spanish Palaeontological Society in Salamanca (Gallemí 1990). Supplementary material has been collected subsequently from this quarry in February 1989 by J. G.

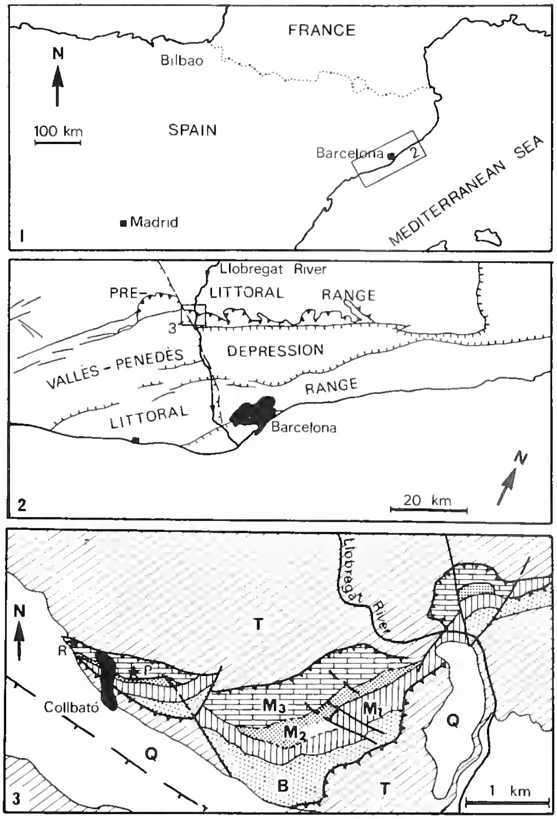
LOCALITY AND GEOLOGICAL SETTING

The holothurians described here come from a steeply dipping bedding surface in an abandoned limestone quarry locally known as 'La Pedrera d'en Rogent' (Rogent's quarry), some 200 metres east of the village of Collbató, Catalonia, north-eastern Spain (Text-fig. 1). It is Middle Triassic in age and represents the most westerly outcrop of Triassic in the Llobregat River area. Collbató is situated in the 'Pre-littoral Range', the innermost of the three tectonic belts into which the Catalan Mountain Ranges are divided; the others being the Vallès-Penedès Depression and the Littoral Range (Text-fig. 1). In the region of Collbató the succession is tectonically complex.

The Triassic of this region overlies Palaeozoic basement and resembles the succession seen in southern Germany with Buntsandstein facies succeeded by Muschelkalk facies. Three units (M1–M3) are recognized within the Muschelkalk here. The upper and lower units (M1 and M3) are carbonates clearly of marine origin, while the middle unit (M2) is composed mainly of sandstones and clays of continental facies. Masachs (1981) had previously suggested that beds equivalent to those at La Pedrera d'en Rogent belong to the M1 unit (Anisian). However, in the most recent geological mapping of this region (Rosell *et al.* 1975), the outcrop at Collbató was placed within unit M3 (Ladinian) and Calzada and Gutiérrez (1988) accepted a Ladinian age for the echinoderm fossil horizon. The holothurian horizon corresponds to the La Riba Reef Formation (F. Calvet, personal communication, July, 1989) and is indeed Ladinian.

Associated fauna at this horizon include sponges, indeterminate internal moulds of gastropods, bivalves, and ammonids, echinoids (some with spines attached) and crinoids. Isolated vertebrae and a single tooth have also been found. The crinoid is a species of *Encrinus* in which the lowest six or seven secundibrachs are uniserially arranged. It comes closest to *E. aculeatus* Meyer, from the Lower Muschelkalk of Germany. The echinoid test material all belongs to *Miocidaris sensu stricto* and the associated spines are of three forms attributable to '*Cidaris*' *wissmanni* Bather [*C. roemeri* of Jekelius (1936) and Mihaly (1981)], '*C.*' *ecki* Assmann and a smooth-shafted, slightly fusiform spine of uncertain affinity. All are relatively long-ranging morphotypes in the Middle Trissic (Smith 1990).

At La Pedrera d'en Rogent 16–20 metres of micritic, finely laminated, almost lithographic, limestones with more marly intercalations are exposed. The section includes at least one layer covered in the trace fossil *Fucoides* and several thin levels of bioclastic limestone, composed largely of echinoderm debris. Sedimentary structures are limited to some megaripples and some scour



TEXT-FIG. 1. Map showing the fossil localities discussed in the text and their regional setting. 1, regional setting and location of map 2. 2, Barcelona region showing position of map 3. 3, simplified geological map of the Collbató district showing the fossil localities (stars) that have yielded holothurians: P = La Pedrera d'en Rogent; R = El Pujolet; T = Tertiary; Q = Quaternary; B = Buntsandstein (Lower Triassic); M1–3 = Lower, Middle and Upper Muschelkalk (Middle Triassic). Simplified from Rosell *et al.* (1975).

troughs associated with bioclastic influx. The detailed succession is very difficult to follow because of the dense network of small-scale faults that cross-cuts the quarry.

Most of the holothurians come from bedding planes that are covered in sponges distributed as small rounded discs or as more continuous mats (Pl. 1, fig. 1). The palaeoenvironment of these precise beds has not been investigated, but Calvet *et al.* (1987) and Calvet and Tucker (1988) have interpreted the palaeoenvironmental setting of the La Riba Reef facies as representing deposition in relatively tranquil marine habitat below fair weather wave-base on an intracratonic carbonate ramp.

A second quarry, 'El Pujolet' lies just to the north west of the village of Collbató (Text-fig. 1). Here a steeply-dipping bedding surface covered in *Fucoides* dominates nearly all of the quarry face. *Encrinus* and ophiuroids have been collected from here, but as yet only a single articulated holothurian (*Strobilothyone rogenti*) has been found.

SYSTEMATIC PALAEONTOLOGY

Class HOLOTHUROIDEA
Order DENDROCHIROTIDA Grube, 1840
Family HETEROTHYONIDAE Pawson, 1970

Diagnosis. Body completely covered in plates lacking spires; spicules in the form of cups may also be present. Plates not pierced for tube feet. Mouth anterior, anus at end of a posterior tail. Calcareous ring composed of five radial and five interradial elements; radial elements not composite, with well developed posterior processes.

Type genus and species. Heterothyone alba (Hutton), from fine sands or muds around New Zealand and the Chatham Islands [Recent].

Taxa included. Strobilothyone rogenti sp. nov. [Middle Triassic, Spain]; *Heterothyone ocnoides* (Dendy) [Recent, New Zealand].

Remarks. S. rogenti clearly belongs to the Dendrochirotida because of its well developed calcareous ring and complete body covering of imbricate plates lacking spires. Pawson (1982) recognized several extant families within this order. Three of these (Phyllophoridae, Sclerodactylidae and Cucumariidae) are soft bodied with their skeleton reduced to microscopic spicules. In addition the former two have complex calcareous rings that are made up of a mosaic of plates, unlike that of *Strobilothyone*. The four remaining families all possess a skeleton of large imbricate plates as does *Strobilothyone*. Psolidae are very easily distinguished because their mouth is displaced dorsally and they have a differentiated sole that is uncalcified: *Strobilothyone* clearly does not belong to that family. Paracucumidae are fully plated and cylindrical in shape but unlike *Strobilothyone* have a simple calcareous ring lacking posterior processes and their plates are spired. Placothuriidae are also fully plated and cylindrical in shape like *Strobilothyone*, but their calcareous ring is very different. Radial elements of the calcareous ring in Placothuriidae have long posterior processes that are composed of a mosaic of small plates. *S. rogenti* comes closest to members of the family Heterothyonidae. Heterothyonids have simple well-defined posterior processes on the radial elements of the calcareous ring that are only slightly shorter than those seen in *S. rogenti*. They are cylindrical in form and fully plated with a slightly differentiated anal tail (Pawson 1970, pl. 1, figs 2 and 3). The family contains only two living species, placed in a single genus, *Heterothyone*. The principal difference between *Heterothyone* and *Strobilothyone* is that in *Heterothyone* there are microscopic ossicles in the form of cups overlying the plates of the body wall. Cups are absent in *Strobilothyone*, which may represent the primitive condition. It is worth noting that in a closely related family, Placothuriidae, there are two species of *Placothuria*, one with scales overlain by microscopic buttons (*P. huttoni* (Dendy)) and the other lacking buttons (*P. squamata* Pawson). Thus the presence of microscopic sclerites in addition to body wall plating appears to be a character of low taxonomic value.

Genus STROBILOTHYONE nov.

Derivation of name. From the Latin *strobilus* a pine-cone, in allusion to its superficial appearance.

Diagnosis. Body plates 1–2 mm broad and undifferentiated; no cup deposits present. Mouth directed ventrally. Anus pentagonal, situated on a posterior tail. Radial elements of calcareous ring with deep anterior notch; posterior processes longer than rest of ossicle.

Type species. Strobilothyone rogenti sp. nov.

Age. Ladinian, Middle Triassic.

Taxonomic remarks. Strobilothyone has a very similar calcareous ring structure to *Heterothyone*, but differs in having a deeper anterior notch in radial elements and slightly longer posterior processes.

EXPLANATION OF PLATE 1

Preservational style of holothurians from the Ladinian at La Pedrera d'en Rogent, Collbató, MGB 32383, × 1. There are eleven specimens of *Strobilothyone rogenti* gen. et sp. nov., including the holotype (arrowed), and a single specimen of *Collbatothuria danieli*, gen. et sp. nov. (C). Small oval masses of sponge cover the surface.

SMITH and GALLEMÍ, *Strobilothyone*, *Collbatothuria*

The principal difference between these two genera is in the complete absence of any spicular deposits in addition to the plates in *Strobilothyone*. In *Heterothyone* cup-elements are present in the body wall (Pawson, 1970, text-fig. 3). Furthermore, in *Strobilothyone*, the mouth appears to be directed slightly ventrally, rather than being terminal as in *Heterothyone*.

Functional morphology and mode of life. This holothurian has an elongate body form with a distinct caudal process which was apparently retractable, since it is not seen in contracted specimens. The mouth and anus open at opposite poles and papillae and other projections are entirely wanting. The smooth vermiform appearance, lack of a clearly differentiated sole and tube feet and the apical position of the mouth all suggest that *Strobilothyone* was an infaunal holothurian. Furthermore, the fact that plates imbricate in two directions (i.e. towards the mouth anteriorly and towards the anus posteriorly) strongly suggests that *Strobilothyone* was U-shaped, since this is precisely the condition seen in modern U-shaped heterothyonids and placothuriids (D. L. Pawson, personal communication, August, 1989). Thus *Strobilothyone* probably lived much like many modern heterothyonids with both anterior and posterior extremities projecting from the sediment (Pawson 1982). Feeding tentacles must have been well developed, to judge from the calcareous ring, and *Strobilothyone* was presumably an infaunal, benthic, suspension-feeder. None of the specimens, however, is preserved in inferred life position, nor is there any evidence of possible holothurian burrows at this horizon.

Strobilothyone rogenti sp. nov.

Plate 1, fig. 1; Plate 2, figs 1–5; Plate 3, figs 1–3; Text-figs 2–6

Types. Holotype MGB 32383 (Pl. 1, fig. 1, arrowed; Pl. 2, fig. 1) paratypes MGB 30556, 30578, 30562, 32320, 32322, 32336, 32338, 32372, BMNH E27540–1.

Other material studied. MGB 30563, 30564 (sectioned), 30566, 30573, 30679–82, 30684 (sectioned), 32321, 32357, 32361, 32364, 32366.

Age and distribution. Middle Triassic, Ladinian, known from La Pedrera d'en Rogent and El Pujolet, near Collbató, Catalonia, north-eastern Spain.

Diagnosis. As for the genus.

Description. Individuals are up to 30 mm in length and are fusiform in shape, the widest point being about mid-length in most cases. The posterior tends to be more pointed than the anterior (Pl. 2, figs 3 and 4; Pl. 3, fig. 3). Some individuals (Pl. 2, fig. 1; Text-fig. 2) have a distinct caudal appendage which is considerably narrower than the rest of the body. This is at most only 25 % of the total length of the body and is absent in obviously contracted specimens (Pl. 3, fig. 1; Text-fig. 3). Contracted specimens are circular in cross-section and there is no differentiated sole. Maximum diameter ranges from about 30–70 % of the length.

The entire body is sheathed in imbricate plates up to 2 mm wide, 0·6 mm in length and about 0·1 mm in thickness. These plates are tightly stacked in contracted specimens (Text-fig. 3) but show much less overlap in extended specimens (Text-fig. 2). They appear to be only two or three stereom layers thick. Most specimens

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EXPLANATION OF PLATE 2

Figs 1–5. *Strobilothyone rogenti* gen. et sp. nov. 1, MGB 32383 (specimen arrowed in Pl. 1, fig. 1), holotype, × 4 (see Text-fig. 2 for interpretation). 2, MGB 30562, paratypes, × 4 (see also Text-fig. 3); note the change in the direction of imbrication between the oral and anal poles. 3, MGB 32338, paratype, almost complete specimen showing anal appendage in contracted state, × 2. 4, MGB 32372, paratype, a juvenile, × 4. 5, MGB 32320, paratype, showing calcareous ring in side view, × 4 (see Text-fig. 4 for interpretation).

All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.


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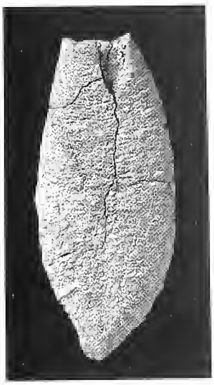
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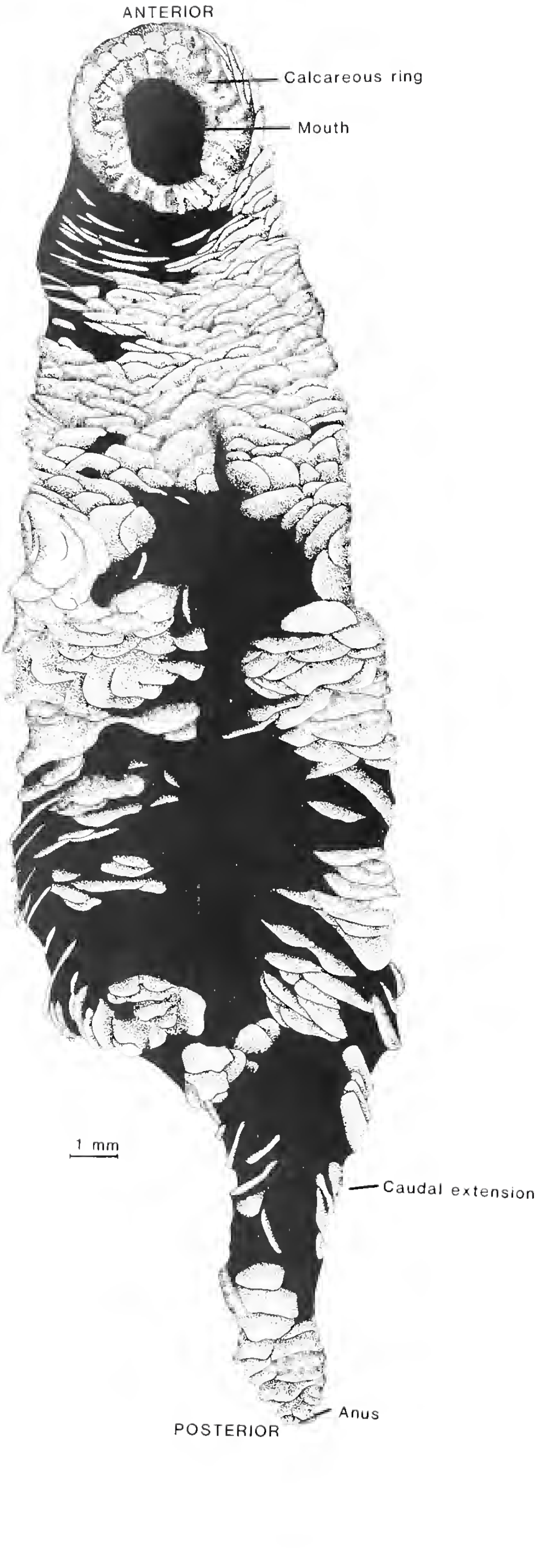
SMITH and GALLEMÍ, *Strobilothyone*



TEXT-FIG. 2. *Strobilothyone rogenti* gen. et sp. nov., MGB 32383; camera lucida drawing of the holotype (see also Pl. 2, fig. 1). Relatively uncontracted specimen in ventral view showing anal appendage.

TEXT-FIG. 3. *Strobilothyone rogenti* gen. et sp. nov., MGB 30562; camera lucida drawing of paratype (see Pl. 2, fig. 2). Specimen in contracted state.

show a change in the sense of imbrication about mid-length, plates towards the anterior imbricate backwards while those in the posterior half imbricate towards the anterior (Pl. 2, fig. 2; Pl. 3, fig. 3; Text-figs 2 and 3). The plating close to the anus becomes virtually pentagonal in some specimens (Pl. 3, fig. 1; Text-fig. 6) suggesting that there might be a pentagon of internal, anal valve plates making this region more rigid. No other spicules are associated with the body wall.

The calcareous ring is seen in MGB 30578 (Pl. 3, fig. 2) and MGB 32320 (Pl. 2, fig. 5). It consists of ten elements, five radial and five interradial pieces (Text-figs 4 and 5). The radial pieces are the larger and have both anterior and posterior processes. Anterior processes are relatively short and two or three in number. The posterior processes are much longer, forming more than half of the radial length of the ossicle. There are two processes to each element and these are simple. The interradial pieces are as broad as the radial pieces but lack posterior processes. They have a small central anterior projection and possibly an adjacent anterior notch.

A small plate about 0·3 mm in diameter with a spongy appearance is seen close to the calcareous ring in MGB 30578 (Text-fig. 5). This may be the madreporite.

Family PSOLIDAE Perrier, 1902

Diagnosis. Plated dendrochirotes with a differentiated sole and both mouth and anus opening on the dorsal surface. Calcareous ring simple; radial elements with shallow anterior notch but without posterior processes.

Subfamily MONILIPSOLINAE nov.

Diagnosis. Body oval in outline and flattened, with double marginal row of stout, perforate bead-like ossicles arranged radially. No oral valve plates.

Type species. Monilipsolus mirabilis sp. nov.

Age. Middle Triassic, Ladinian.

Remarks. This subfamily is erected for the new species *Monilipsolus mirabilis.* It is fully plated with differentiated dorsal and ventral plating, the ventral surface taking the form of a sole. In general body organization it closely resembles extant psolid dendrochirotes, having the mouth displaced dorsally and the anus also dorsal and at the end of a short tail. The calcareous ring of *Monilipsolus* resembles that of living psolids, being composed of radial and interradial elements that are moderately stout and lack posterior processes. The presence of an almost complete plated integument over the peristome and a solid calcareous ring suggests that *Monilipsolus* possessed an introvert and could withdraw its tentacles. *Monilipsolus* differs from extant psolids in having a strongly calcified sole and in having a remarkable double ring of stout, perforate, bead-like ossicles around the periphery. This last character easily distinguishes *Monilipsolis* from all extant species of Psolidae and is an excellent autapomorphy for the subfamily.

Genus MONILIPSOLUS nov.

Derivation of name. From the Latin *monile*, a necklace, in allusion to the appearance of the peripheral band of bead-like ossicles.

Type species. Monilipsolus mirabilis sp. nov.

Age. Middle Triassic, Ladinian.

Diagnosis. Body oval, up to 55 mm in length and about $\frac{1}{3}$rd as wide; depressed. Sole of thin imbricate plates; dorsal surface of thicker plates with two irregular biserial bands of single pores perforating plates. Tube-feet absent from sole but probably present around margin. Peristome large, occupying most of the anterior end of the dorsal surface, largely covered by a peristomial membrane of radially-arranged plates. Periproct at end of small tail. Well developed anterior notch on radial elements of calcareous ring.

Description. See description of *M. mirabilis* below.

Remarks. Monilipsolus is a most remarkable holothurian genus. No other holothurian possesses any structure comparable with the large perforate calcite ossicles that rim the body. The function of these ossicles is unknown. It seems probable that *Monilipsolus* was a suspension feeder, like modern psolids, since it has a dorsally directed mouth and ventral sole for attachment. The large size of the

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EXPLANATION OF PLATE 3

Figs 1–3. *Strobilothyone rogenti* gen. et sp. nov. 1, MGB 32322 (paratype), juvenile (see also Text-fig. 6). 2, MGB 30578 (paratypes); two specimens, the lower of which shows part of the calcareous ring (see Text-fig. 5). 3, MGB 30556 (paratype). All ×4.

Fig. 4. *Collbatothuria danieli* gen. et sp. nov., MGB 32274 (paratype), ×3 (see also Text-fig. 18).

All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.

PLATE 3


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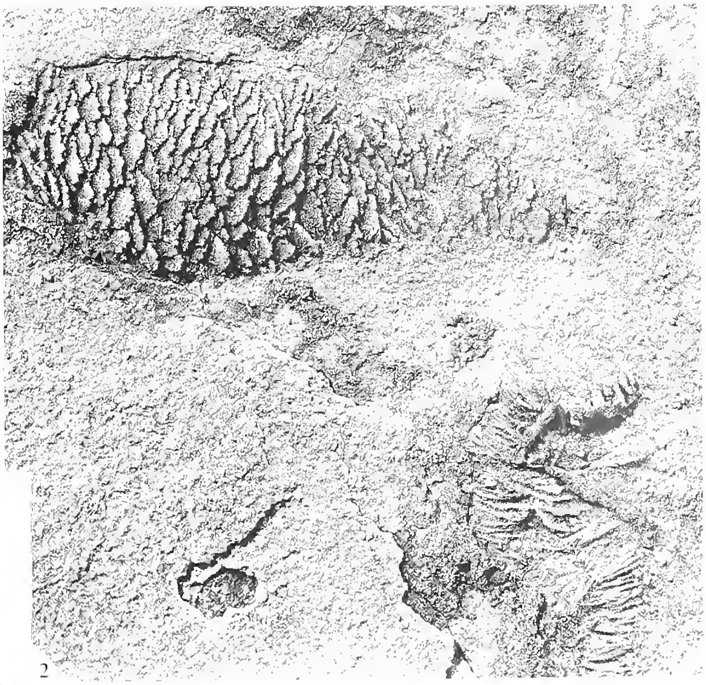
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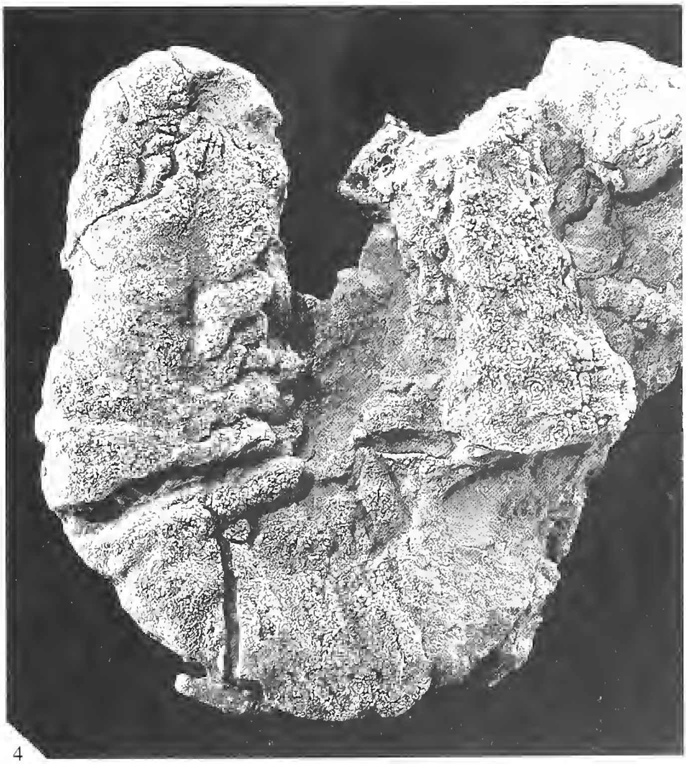
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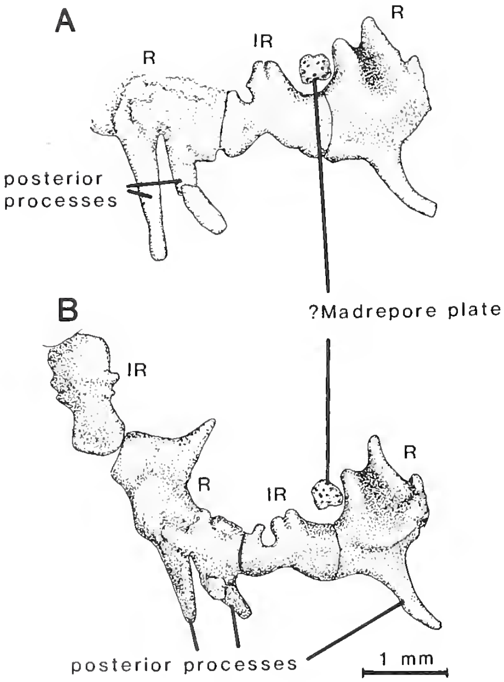
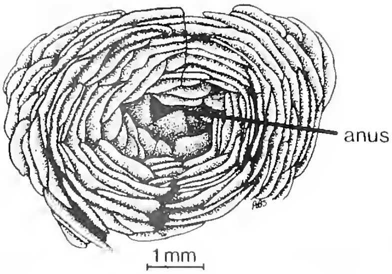
SMITH and GALLEMÍ, *Strobilothyone*, *Collbatothuria*

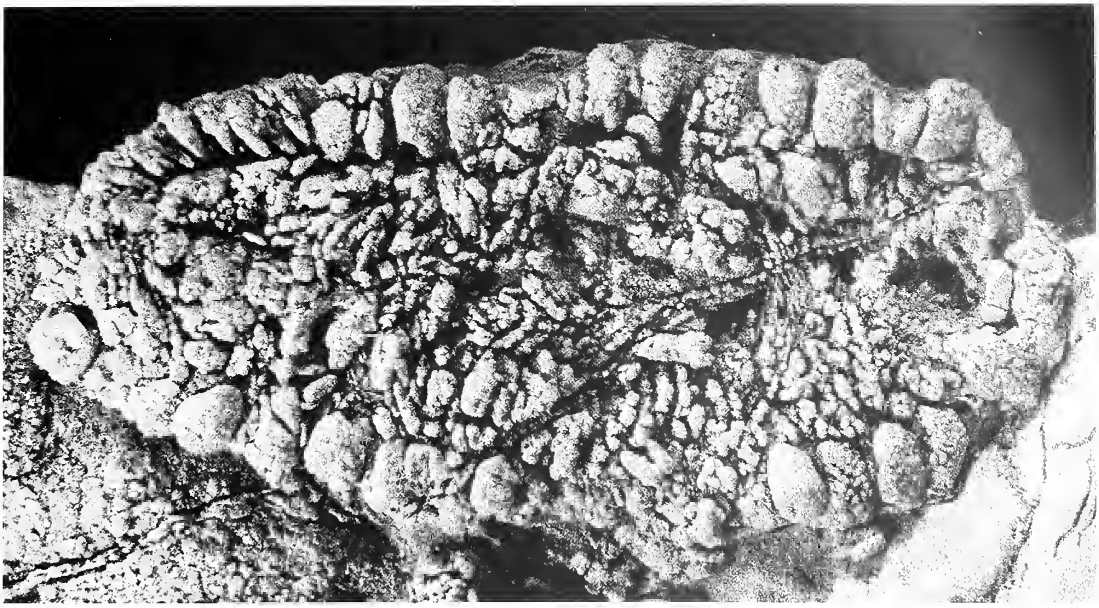
TEXT-FIG. 4. *Strobilothyone rogenti* gen. et sp. nov., MGB 32320; camera lucida drawing of paratype (see Pl. 2, fig. 5). Anterior portion showing the calcareous ring elements in side view; note the apical position of the mouth.



TEXT-FIG. 5. *Strobilothyone rogenti* gen. et sp. nov., MGB 30578; paratype: camera lucida drawings of calcareous ring elements in a partially disarticulated specimen. A, lateral aspect showing two radial (R) and one interradial (IR) elements. B, same in more anterior aspect. Both to same scale.

TEXT-FIG. 6. *Strobilothyone rogenti* gen. et sp. nov., MGB 32322; paratype. Camera lucida drawing of the posterior region showing the anus and the pentagonal arrangement of plates surrounding it (see Pl. 3, fig. 1).



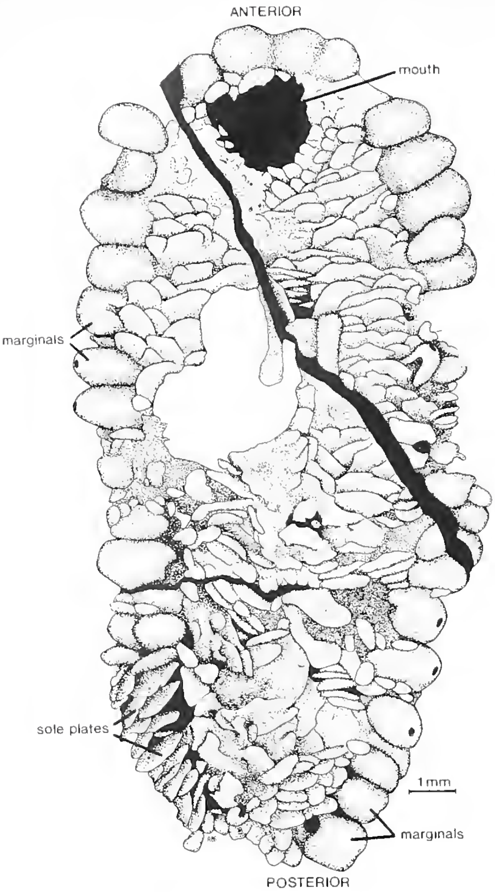


TEXT-FIG. 7. *Monilipsolus mirabilis* gen. et sp. nov., MGB 32385, holotype; dorsal surface, × 8. See Text-fig. 8 for an interpretation.

peristome, the fact that it is mostly covered by a flexible plated membrane, and the presence of a well developed calcareous ring whose radial elements have deep anterior notches for the attachment of tentacle retractor muscles all point to there being an introvert; the tentacles could presumably have been more or less fully retracted and protected by the peristomial plated membrane. The periproct lies on the dorsal surface at the end of a short tail. The flattened profile and broad, differentiated sole suggest that *Monilipsolus* was adapted to grip onto firm or hard bottoms. Oral tube-feet may have been present but uncalcified, or might have been absent; none is preserved. However, there are rather large circular spaces found around the periphery of the sole, adjacent to each perforate ball, which might mark the sites of large tube-feet (Text-figs 13 and 14). Tube feet were definitely present dorsally, but were small and have not been preserved. There are two irregular bands of small perforations, about 0·1 mm in diameter, on dorsal plates that run along the length of the animal (Text-fig. 12) and which mark the site of the tube feet.

Thus in general body organization and mode of life *Monilipsolus* closely resembles modern psolid, suspension feeders which cling to pebbles and other such solid substrata.

The stout perforate ossicles that form a marginal rim to *Monilipsolus* are unique and of unknown function. These are sometimes slightly faceted to fit closely together and are developed around the



TEXT-FIG. 8. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 32385 (holotype), dorsal aspect (see Text-fig. 7).

entire periphery, without a break. The perforations are narrow, 0·5–0·6 mm in diameter in ossicles 1·5–1·6 mm in diameter and expand slightly towards the interior. The interior opening of these pores lies within the body cavity, inside the plated mesoderm, and so must have connected to some internal coelom or organ. The exterior opening is directed laterally and slightly downwards (ventrally), so that it is generally not seen in dorsal view and can just be seen in ventral view.

The functional significance of this peripheral ring of perforate ossicles can be assessed by considering its possible role with respect to the various vital functions that a holothurian must perform. These are to do with feeding, sensory reception, defence, locomotion/adhesion, reproduction and respiration.

It seems highly improbable that the perforate ossicles played any part in feeding since they are well removed from the mouth and digestive tract. Comparative morphology suggests that *Monilipsolus* fed using tentacles, like psolids.

EXPLANATION OF PLATE 4

Figs 1–3. *Monilipsolus mirabilis* gen. et sp. nov. 1, MGB 32367 (paratypes); both individuals show dorsal surfaces (incomplete), the upper is illustrated in Text-fig. 11. 2, MGB 30671 (paratype), dorsal surface showing tube foot pores (see also Text-fig. 12). 3, MGB 32325 (paratype), dorsal surface, mouth to the left (see Text-fig. 10 for interpretation). All × 3.

All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.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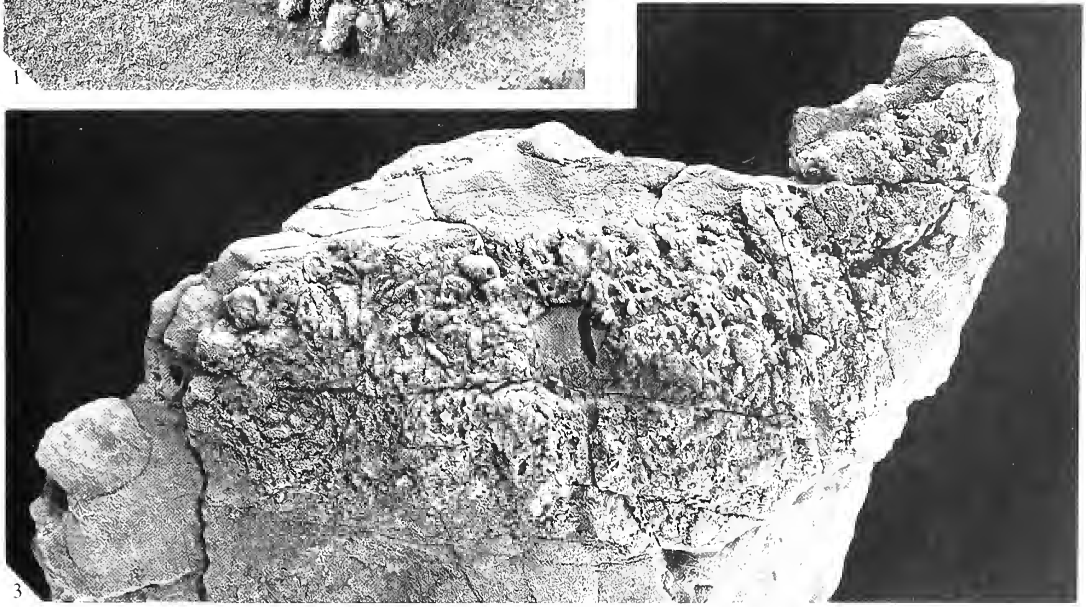
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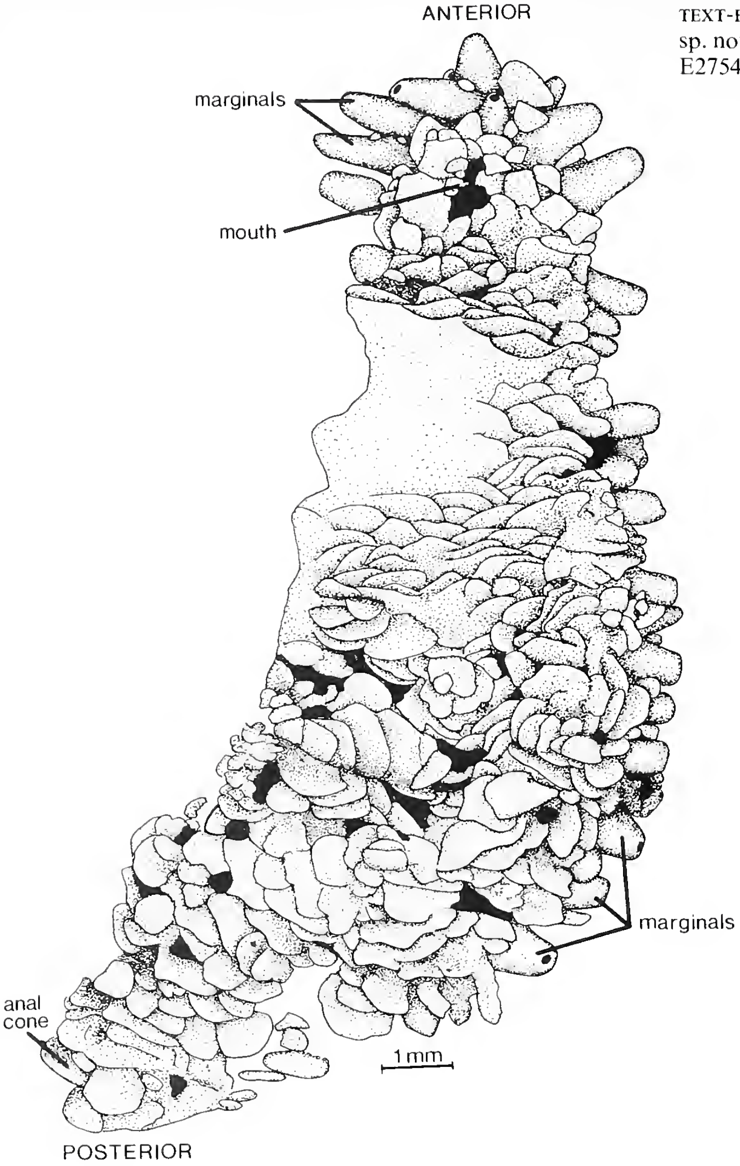
SMITH and GALLEMÍ, *Monilipsolus*

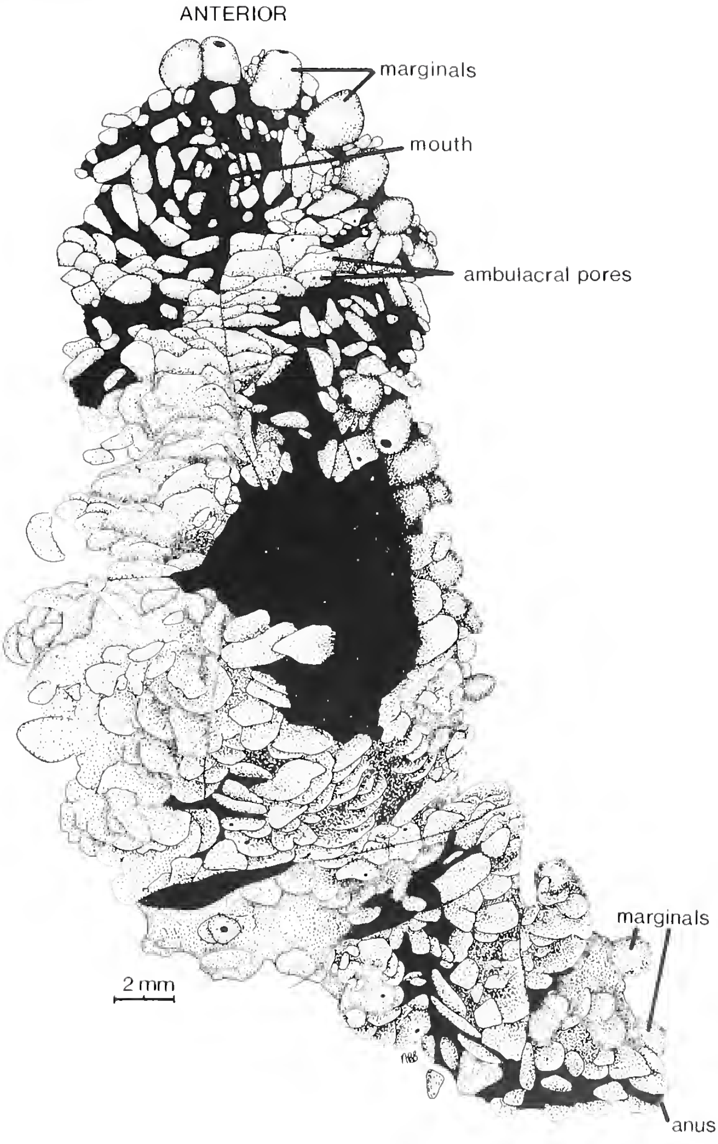


TEXT-FIG. 9. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of BMNH E27543; paratype (see Pl. 5, fig. 2). Dorsal surface.

They are also almost certainly not associated with reproduction, simply because of their multiplicity and distribution around the entire periphery. In holothurians the gonads open through a single pore close to the tentacle ring. No holothurian has multiple gonopore openings and their distribution and orientation are difficult to explain in functional terms.

Gaseous exchange is another possible function. The pores would then be inhalant or exhalant (or both) orifices through which sea water would be drawn inside the mesodermal skeleton to allow efficient gaseous exchange, presumably across a thin membrane. Although some Palaeozoic cystoids have developed a comparable system, no holothurian is known that has any system remotely comparable. Furthermore, the positioning of the pores around the periphery of the animal pointing

TEXT-FIG. 10. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 32325; paratype (see Pl. 4, fig. 3). Dorsal aspect.



slightly downwards would only make sense if these were exhalant orifices and no obvious inhalant orifice can be identified. We do not favour this interpretation.

They cannot be locomotory in function, because they have no articulation at the base and seem to fit together very closely, often being slightly facetted. The perforations might conceivably be associated with some form of secretion to enhance adhesion. However, it must be pointed out that the environment in which *Monilipsolus* is preserved shows no evidence of strong current activity. Another possibility is that they are in some way associated with defence, possibly openings for extruding some form of sticky substance as the Cuverian tubules do. However, although they form a continuous ring around the periphery of the animal, which gives all round protection, the openings are directed slightly downwards and one might expect structures associated with defensive secretions to be scattered over the entire dorsal surface rather than being restricted to the very periphery.

The most likely interpretation is that these structures were sensory in function, for example housing long tube-feet that formed a sensory frill around the entire margin of the animal. However, this fails to explain why the ossicles themselves are so massive and we assume that tube-feet were needed to provide grip and on the ventral surface were directed downwards, not laterally.

The stout perforate ossicles that rim this species are highly distinctive and should be recognizable even from disarticulated debris. Interestingly, no such ossicles have ever been recorded from the St Cassian Beds (Cassian, late Middle Triassic) of the Cortina d'Ampezzo district of Italy, where a very rich echinoderm fauna has been documented by Zardini (1976). Zardini has carefully identified a large number of isolated skeletal elements, many of them very small, including echinoid spines, asteroid and ophiuroid ossicles, crinoid columnals and even somphocrinid cups. The absence of monilipsolid ossicles in the St Cassian Beds is thus unlikely to be due to collection failure.

Monilipsolus mirabilis sp. nov.

Pate 4, figs 1–3; Plate 5, figs 1–4; Text-figs 7–14

Diagnosis. As for the genus.

Types. Holotype MGB 32385 (Text-fig. 7); paratypes MGB 30561, 30565, 30569, 30572, 30576, 30671, 30674, 32319, 32325, 32367, 32384, BMNH E27542–3.

Other material studied. MGB 32365, 32369 (sectioned).

Age and distribution. Middle Triassic, Ladinian, known only from La Pedrera d'en Rogent, Collbató, Catalonia, north-eastern Spain.

Description. Body flattened in profile and oval in outline with the skeleton differentiated into a lower (ventral) sole of thin imbricate plates, a marginal band of stout perforate ossicles arranged into two irregular rows anteriorly, and an upper domed surface of thicker imbricate plates some of which are perforated for tube feet. Individuals range from about 25 mm long by 8 mm wide to 55 mm by 18 mm. Anterior and posterior end are uniformly rounded, the anterior (Pl. 5, fig. 1) being generally slightly wider than the posterior (Pl. 5, fig. 3). The body is usually parallel-sided but tapers slightly in the posterior third (Text-figs 9 and 10).

The ventral surface is composed of a series of thin, imbricate plates that are laterally elongate (Pl. 5, figs 1, 3, 4). Plates are widest down the median part of the sole and become more equant in outline towards the edge (Text-fig. 13). Very rarely one or more of the sole plates around the margin may be perforated like the marginal ossicles (Text-fig. 14). The ventral plates usually have a high degree of overlap and imbricate towards the posterior. None of the ventral plates is perforated for tube feet but around the edge of this surface, immediately adjacent to the stout marginal ossicles, are found small (0·3 mm) gaps that in places appear almost circular. These may mark the sites of ventral tube feet. Although no definite remains of tube feet are preserved, vague tubular structures in between marginal ossicles (Text-fig. 14) may possibly represent tube feet.

Marginal ossicles are shaped like the beads of a necklace and are slightly tapered distally (Pl. 4, fig. 1). In larger individuals these ossicles are about 2·0–2·3 mm in length and 1·1–1·2 mm in width. Each is perforated by a 0·5 mm diameter cylindrical pore that expands very slightly towards the interior. The ossicles have a smooth surface and form a continuous ring to the margin of the body (Text-fig. 8). They are irregularly arranged into

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EXPLANATION OF PLATE 5

Figs 1–4. *Monilipsolus mirabilis* gen. et sp. nov. 1, MGB 30674 (paratype), ventral surface, anterior to top. 2, BMNH E27543 (paratype), juvenile, dorsal surface, anterior to the right (see also Text-fig. 9). 3, MGB 30576 (paratype), ventral surface, posterior to top (see also Text-fig. 13). 4, MGB 30561 (paratype), ventral surface, anterior portion, (see also Text-fig. 14). All ×4.

All specimens from the Ladinian, Middle Triassic at La Pedrera d'en Rogent, Collbató, north-eastern Spain.


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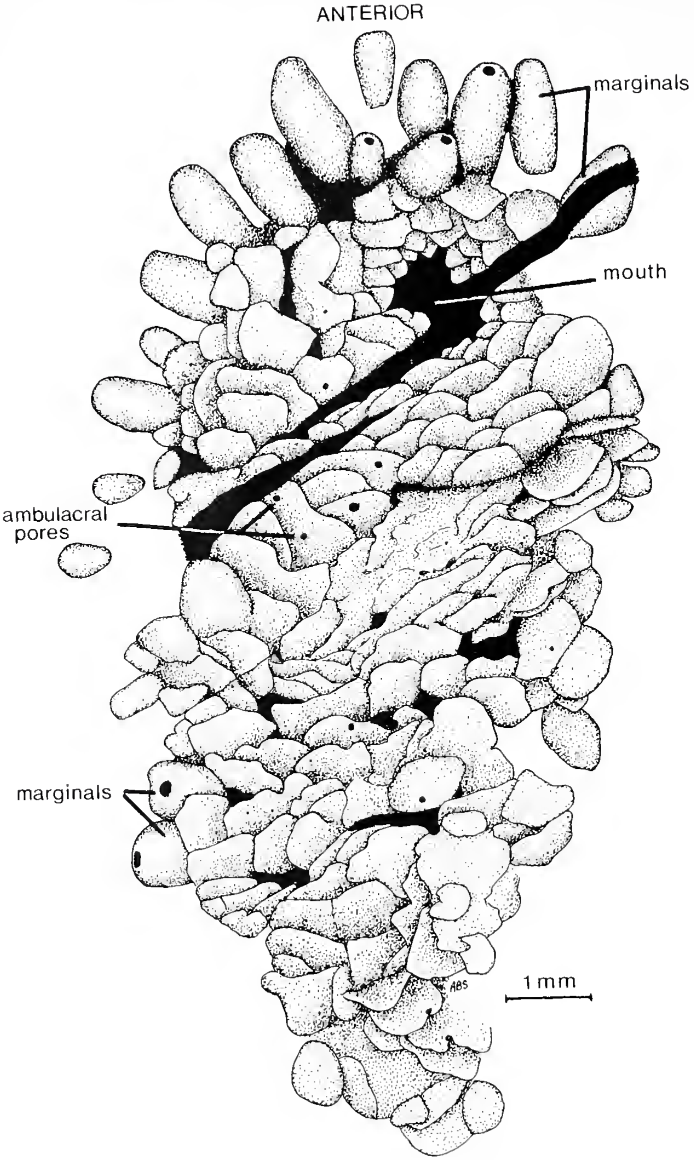
SMITH and GALLEMÍ, *Monilipsolus*

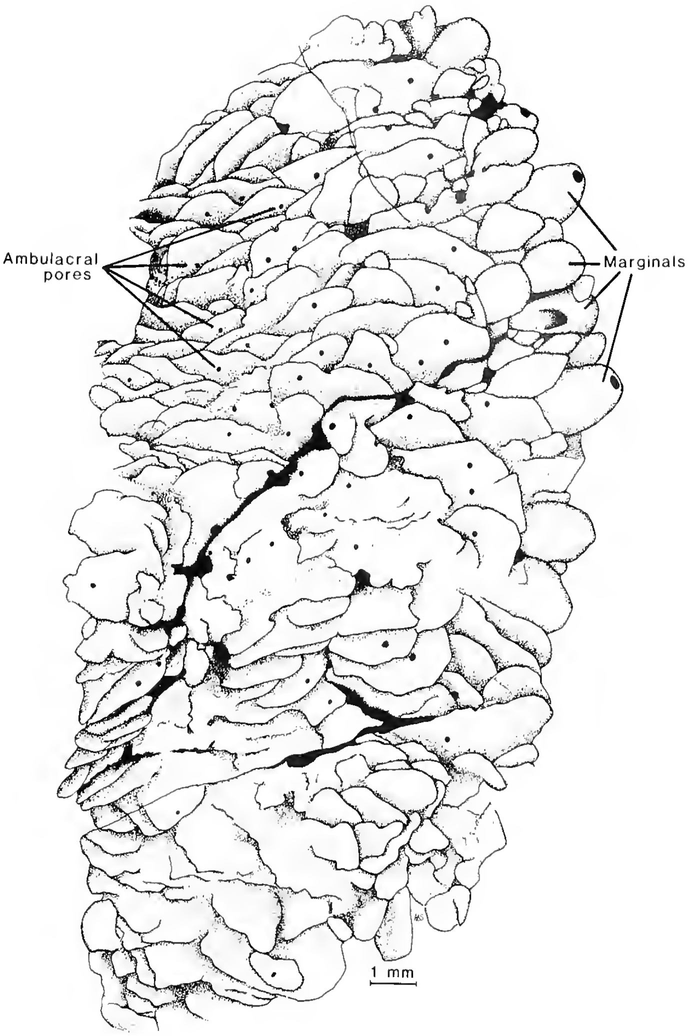


TEXT-FIG. 11. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 32367; paratype (see Pl. 4, fig. 1). Anterior portion seen in dorsal aspect showing peristome and tube foot pores.

an upper and lower alternating series, but this becomes better defined around the anterior and posterior borders where two distinct rows of marginals are present (Text-fig. 11). The pores on marginal ossicles open distally and are usually just visible in ventral aspect (Pl. 5, fig. 4) but not in dorsal aspect (Pl. 4, fig. 1).

The dorsal surface was domed in life but is now usually collapsed. It is composed of imbricate plates that are thicker than those of the sole (about 0·15–0·2 mm in thickness) and show a much smaller degree of overlap (Text-figs 11 and 12). There is no recognizable organization to this surface. Both the mouth and anus lie on this surface. The peristome is recognizable as a large area of concentrically arranged platelets around a central hole situated close to the anterior (Pl. 4, figs 1 and 3; Text-figs 7–11). Platelets decrease in size towards the opening and there are no larger valve-like plates protecting the mouth. The peristome occupies most of the anterior end of the body. The anus lies near the posterior end of the body and in some specimens appears to form a small tail-like projection (Text-figs 9 and 10; Pl. 4, fig. 3; Pl. 5, fig. 2). In between the peristome and anal tail many of the dorsal plates are perforated for tube feet (Pl. 4, fig. 2; Text-figs 11 and 12). These pores

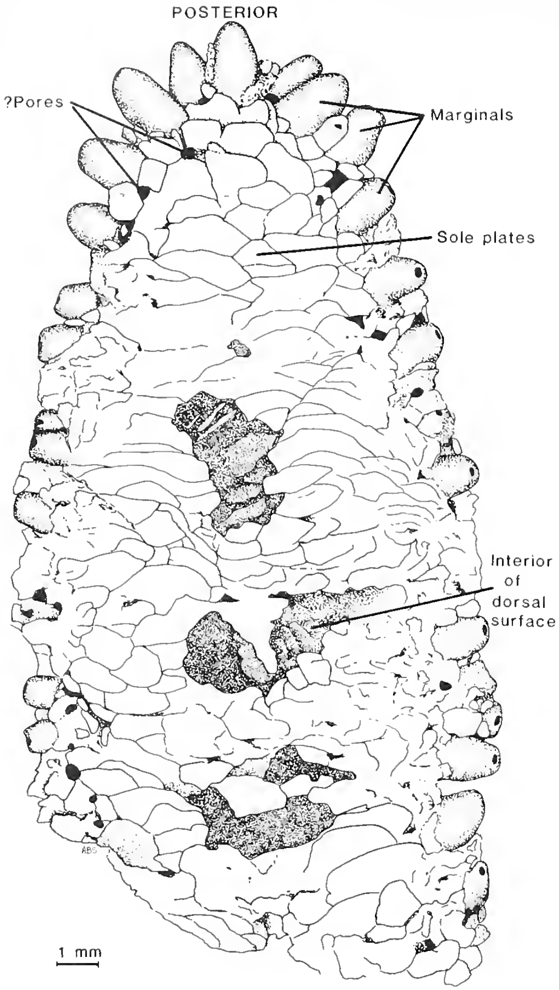
TEXT-FIG. 12. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of dorsal plating in MGB 30671 (paratype) showing the distribution of the tube foot pores (see Pl. 4, fig. 2).



are more or less scattered over the entire surface with a tendency to be concentrated into two bands, one on each side of the mid-line (Text-fig. 12).

The complete calcareous ring is not seen in any specimen but elements of it are exposed in a slightly disaggregated specimen, MGB 30674. The interradial elements are narrow and spade-shaped, lacking posterior processes but with a large anterior projection. The radial elements are broader than long and also lack posterior processes, the posterior border being distinctly concave. There is a moderately deep anterior notch centrally which in effect defines two small anterior processes. This notch may in fact become closed over anteriorly so as to form a pore.

Remarks. Like other holothurians from this locality, specimens of this species commonly display a mid-ventral groove due to early diagenetic compaction and collapse of the skeleton above the digestive tract.



TEXT-FIG. 13. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 30576; paratype (see Pl. 5, fig. 3). Ventral surface showing sole plating.

Order ASPIDOCHIROTIDA Grube, 1840
Family uncertain
Genus COLLBATOTHURIA nov.

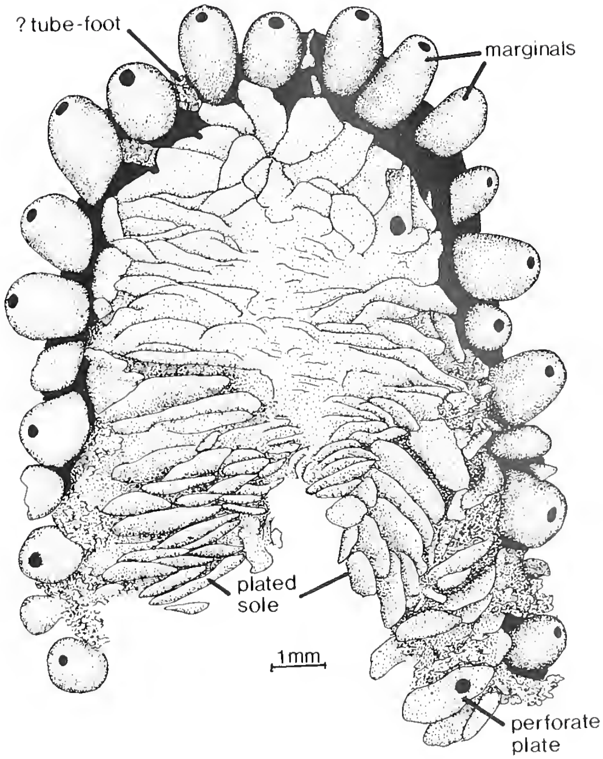
Derivation of name; after the village of Collbató near where the species was found.

Type species. *Collbatothuria danieli* sp. nov.

Age and distribution. Middle Triassic, Ladinian, known only from La Pedrera d'en Rogent, Collbató, Catalonia, north-eastern Spain.

Diagnosis. Small (up to 50 mm in length), vermiform, differentiated dorso-ventrally into a sole with many tube-feet and a latero-dorsal surface lacking tube-feet and without warts. Mouth large, open, at anterior but slightly ventral. Anus at posterior terminus. Body wall thick and heavily calcified but not plated. Form of body-wall spiculation unknown. Calcareous ring present, but form unknown; apparently simple without anterior projections.

TEXT-FIG. 14. *Monilipsolus mirabilis* gen. et sp. nov., camera lucida drawing of MGB 30561; paratype (see Pl. 5, fig. 4). Ventral surface showing sole plating and marginals.



Remarks. The systematic position of this genus remains uncertain. Its thick wrinkled body wall, obviously heavily calcified with spicules, its straight cylindrical body and differentiated sole, and simple calcareous ring are all suggestive of Aspidochirotida. Three families are currently recognized within the Aspidochirotida (Pawson 1982), but unfortunately they are differentiated solely on soft tissue, anatomical structures (arrangement of gonads, presence/absence of tentacle ampullae). It is therefore impossible to be more specific about the taxonomic placement of *Collbatothuria*. In general body form and organization it resembles several genera within the Holothuriidae and Stichopidae. *Collbatothuria* has relatively smooth dorsal and lateral surfaces with only circumferential crenulations associated with contraction. Wart-like projections are absent from dorsal and lateral surfaces and there is also no evidence of tube feet in this region, though they are clearly developed over the sole. These characters differentiate *Collbatothuria* from extant genera of Holothuriidae and Stichopidae.

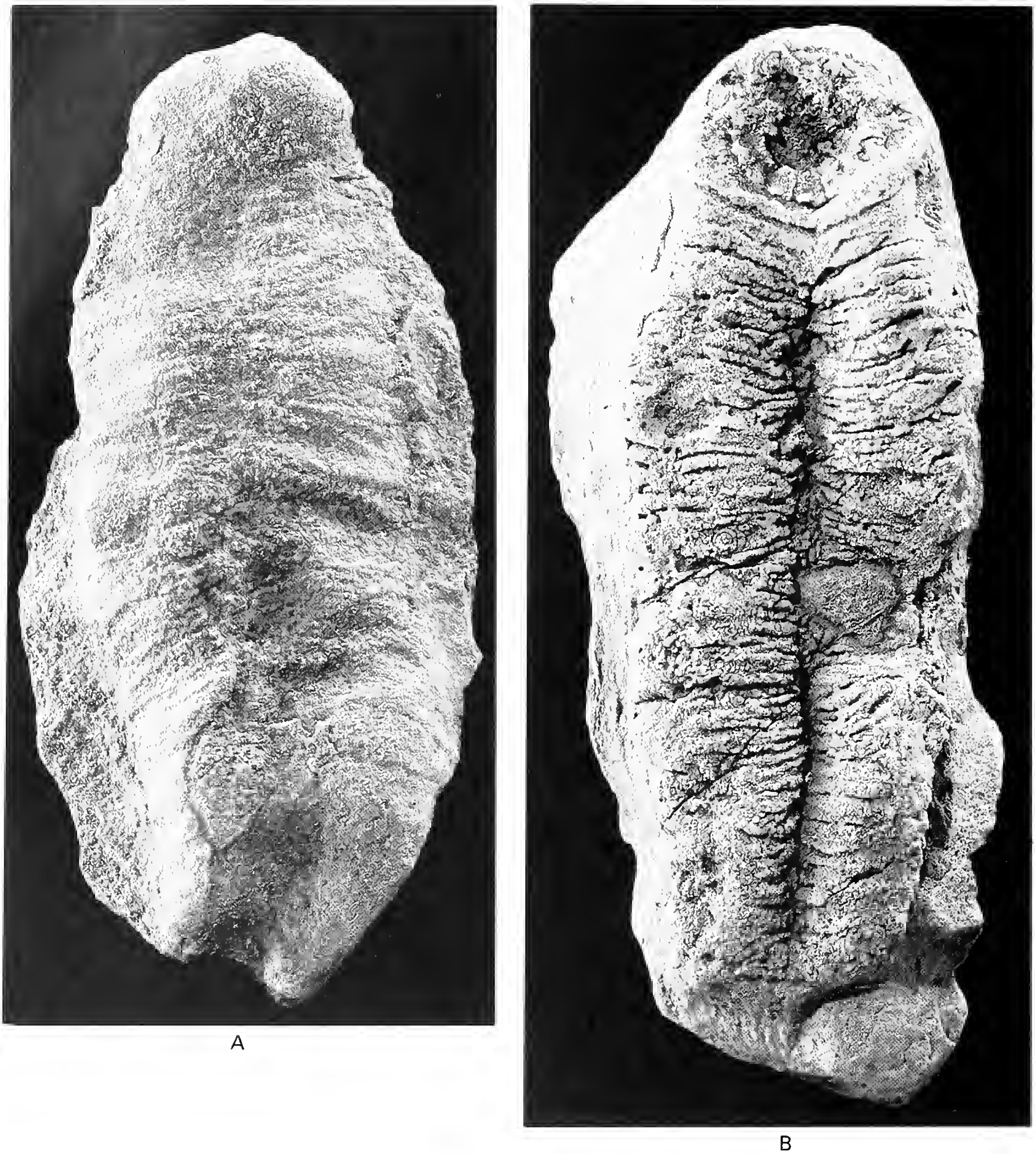
The well differentiated sole with its numerous tube feet indicate that *Collbatothuria* was an epifaunal benthic crawler with a locomotory sole. Its downward-opening mouth suggests that it was a deposit-feeder, using its tentacles to pick up suitable detritus from the sea floor. Its mode of life was, therefore, similar to that of modern Holothuriidae and Stichopidae.

Collbatothuria danieli sp. nov.

Plate 3, fig. 4; Text-figs 15–18

Derivation of name; in honour of Dr Daniel Gutiérrez, an amateur palaeontologist who discovered the holotype and other specimens.

Diagnosis. As for the genus.



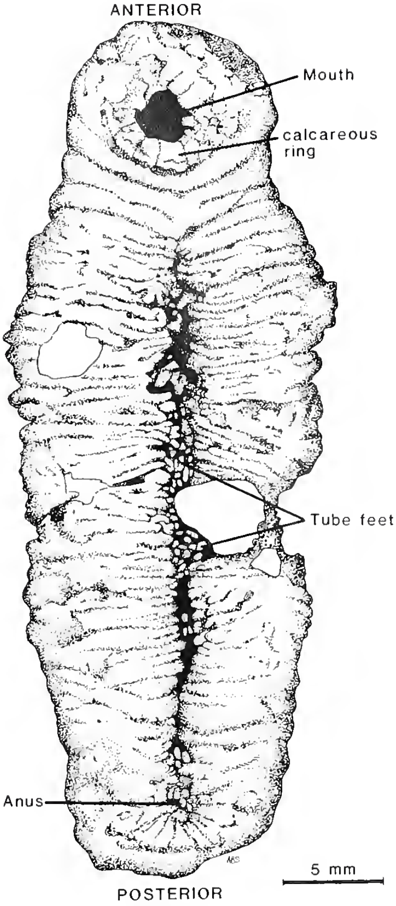
TEXT-FIG. 15. *Collbatothuria danieli* gen. et sp. nov.; A, dorsal surface, BMNH E27544 (see Text-fig. 17); B, ventral surface of holotype, MGB 32273 (see Text-fig. 16). Both specimens ×4.

Types. Holotype MGB 32273; paratypes MGB 32274, 32377, 32383 (Pl. 1, fig. 1; 'C'), BMNH E27544.

Age and distribution. Middle Triassic, Ladinian, known only from La Pedrera d'en Rogent, Collbató, Catalonia, north-eastern Spain.

Description. Specimens, which are sausage-shaped, are 35 mm to 52 mm long. They were presumably ovoid in cross-section, but are now flattened due to diagenetic compression with a median furrow marking the digestive tract (Text-fig. 15). Their overall shape varies with the state of contraction. Contracted specimens are rather

TEXT-FIG. 16. *Collbatothuria danieli* gen. et sp. nov., camera lucida drawing of MGB 32273 (holotype). Ventral surface.

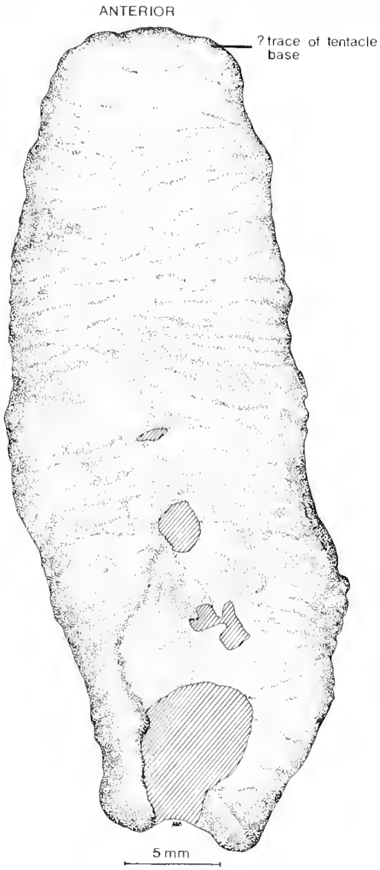


short and fat, with a maximum width that is almost 50% of the length (Pl. 1, fig. 1; 'C'). Others are more elongate with a width that is only about 20% of the length (Pl. 3, fig. 4). One specimen is preserved in a U-shaped position (Text-fig. 18), but other specimens are all straight.

The mouth lies anteriorly facing downwards (Text-figs 15 and 16). It is a large circular opening, some 2·5 mm in diameter in a 35 mm long specimen. This opening is surrounded by a ring-like structure of individual elements which represents the calcareous ring (Text-fig. 16). The precise structure of the calcareous ring cannot, however, be made out since it is covered by thick integument. There appear to be only ten elements and none has strong anterior projections. There is no visible body wall plating, the body being a wrinkled integument (Pl. 3, fig. 4; Text-fig. 15). This integument is relatively thick and presumably must have been heavily spiculated to be preserved, but the silicification has destroyed any original spicules that were present. The dorsal surface is virtually smooth and wrinkle-free (Text-figs 15A and 17) and has no papillae, tube feet or warty projections. The ventral surface is generally concave and presumably contracted prior to death. It is differentiated as a sole and there are numerous small tube feet on this surface (Text-figs 15B, 16). The ventral surface is much more strongly wrinkled than the dorsal surface and papillae are well developed along the margin of the sole (Pl. 3, fig. 4; Text-fig. 18). The anus is terminal and in MGB 32273 is marked by a concentric valvular appearance to the integument (Text-figs 15B and 16). In MGB 32274 there appear to be a few larger papillae developed around the anus (Text-fig. 18).

EVOLUTIONARY IMPLICATIONS OF THE FAUNA

The Collbató fossil bed is uniquely important in yielding a fauna of holothurians in relative

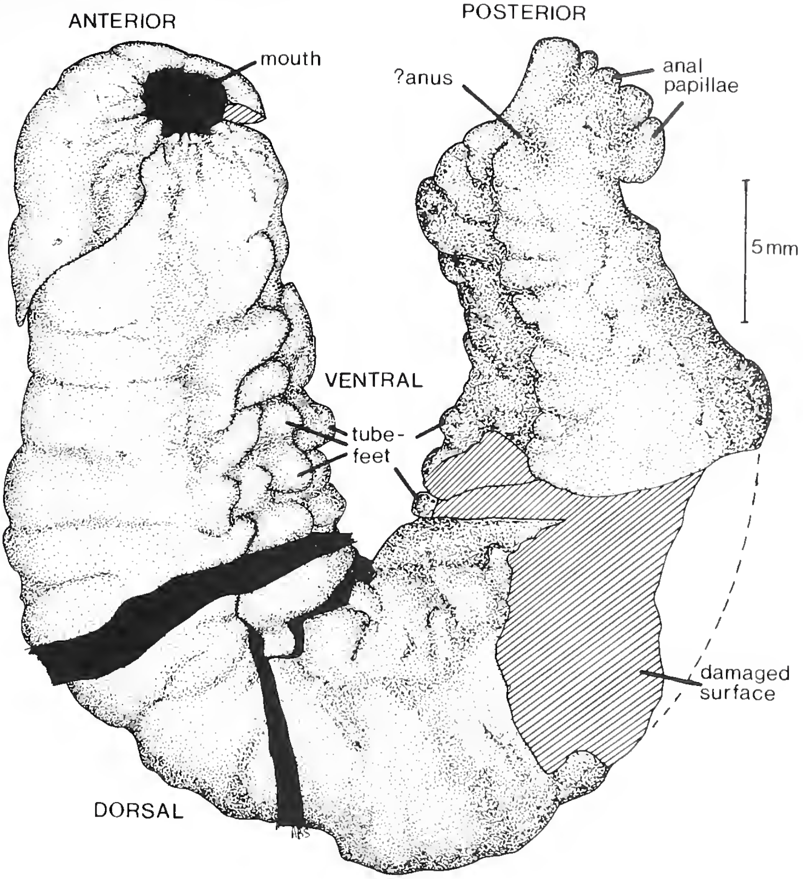


TEXT-FIG. 17. *Collbatothuria danieli* gen. et sp. nov., camera lucida drawing of BMNH E27544 (paratype). Dorsal surface: cross-hatching = sediment covered areas.

abundance, belonging to three separate families. What is more, these are by far the best preserved, complete specimens of fossil holothurians that have ever been discovered. Only in one other fossil holothurian can details of general anatomical arrangement, body-wall plating and the structure of the calcareous ring be documented and that is the synaptid apodan *Achistrum* from the Middle Pennsylvanian of Illinois. The information available on these species makes it possible to place them within a biological classification established on Recent species with a fair degree of certainty.

Two other species, *Oneirophantites tarragonensis* Cherbonnier and *Bathysynactites viai* Cherbonnier, have been reported from the Middle Triassic of Tarragona, Spain (Cherbonnier 1978). Neither is well preserved or reveals as much anatomical information as the three species described here, since they are preserved only as decalcified impressions. However, *Oneirophantites* was tentatively assigned to the order Elasipoda on account of its long lateral papillae and the position of the mouth, and *Bathysynactites* was assigned to the Aspidochirotida. Both were preserved in anoxic facies of Middle Triassic (Muschelkalk) age.

Taking the Tarragona and Collbató fossil holothurians together, gives a Middle Triassic fauna of five species. These belong to three orders, namely Elasipodida, Aspidochirotida and Dendrochirotida. Members of a fourth order, Apodida, must have been present since the group had already differentiated by the Upper Carboniferous, as shown by the *Achistrum* sp. from the Mazon Creek Shale. Thus, of the six extant orders of Holothurioida, only Molpadiida and Dactylochirotida have no fossil record by the early Mesozoic. Considerable taxonomic diversity of holothurians had therefore been achieved by the Middle Triassic. Furthermore, a certain amount of ecological



TEXT-FIG. 18. *Collbatothuria danieli* gen. et sp. nov., camera lucida drawing of MGB 32274; paratype (see Pl. 3, fig. 4). Specimen in lateral view with ventral surface towards the interior.

diversification is also evident. In the Middle Triassic we can recognize epibenthic, deposit-feeding forms with well developed soles (*Collbatothuria*, ?*Bathysynactites*, ?*Oneirophantites*), burrowers (*Strobilothyone*) and epibenthic, psolid-like suspension-feeders that attached to firm bottoms (*Monilipsolus*). Considering how well skeletized some of these taxa are and how diverse holothurians had become by the Middle Triassic, it is surprising to us how rarely they have been reported in the fossil record.

Acknowledgements. Field trips have been covered with funds of the MGB's Project 'Work on fossiliferous localities' (1988 and 1989) financed by the Ajuntament de Barcelona (Area de Cultura-Secretaria Technica de Museus). A British Council's Academic Travel Grant allowed one of us (J.G.) to carry out research for the paper. We thank also D. Brusi for presenting the first material from Collbató, Dr J. M. Pons, E. Vicens and J. Muñoz (Universitat Autónoma de Barcelona) for their help in previous phases of the study, Mr E. Rogent for allowing us access to his quarry and D. Gutiérrez, R. Mañé and I. Gurrea for donating important specimens. Dave Pawson, Chris Paul and Paul Gilliland provided helpful comments on an earlier draft of the paper, for which we are grateful.

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A NEW UPPER ORDOVICIAN BRYOZOAN FAUNA FROM THE SLADE AND REDHILL BEDS, SOUTH WALES

by CAROLINE J. BUTTLER

ABSTRACT. A diverse bryozoan fauna has been discovered in South Wales in the Slade and Redhill Beds (upper Rawtheyan, Ashgill), exposed in a new road-cutting near Whitland. This is the first account of a moderately diverse Ordovician bryozoan fauna from Britain. The fauna is represented by 15 species belonging to four orders, the majority being Trepostomata. One new genus is described, *Pinnatoporella* (Fenestrata), and three new species *Heterotrypa sladei*, *Dekayia pengawsensis*, and *Anaphragma gwyndyense* (all Trepostomata). New information has led to the redescription of the cystoporate family Rhinoporidae and its reassignment to the suborder Ceramoporina. Ordovician bryozoans are poorly known in Britain, partly because well-preserved diverse faunas such as this are very rare. The fauna is compared biogeographically with previously described Bryozoa. At generic level it is cosmopolitan; however, approximately half the species are endemic to Wales. The remaining species have greatest affinity with Baltoscandia; species level affinities with North America are poorer.

BRYOZOANS are one of the major components of Ordovician faunas. They have been described extensively from North America and the Soviet Union but have been largely neglected in Britain. This neglect may be attributed partly to poor preservation and the time required to prepare specimens, but it is also due to the lack of any great tradition of research on British Palaeozoic bryozoans. No entire bryozoan fauna has previously been described from a British upper Ordovician locality. Worldwide biogeographical comparisons of Ordovician bryozoans therefore omit Britain.

PREVIOUS RESEARCH ON BRITISH ORDOVICIAN BRYOZOANS

Bryozoans are frequently decalcified in British Ordovician rocks, making them easy to distinguish in the field but hard to identify taxonomically even to family level. In faunal community studies bryozoans are often only identified by their gross morphology, for example 'stick bryozoans' or 'prasoporid', the latter term covering any dome-shaped trepostome. Calcified specimens tend to go unnoticed in the field, except in a few localities such as the Slade and Redhill Beds at Pengawse Hill in South Wales, described herein, where a large proportion of the rock consists of bryozoans.

In major British museums (e.g. Natural History Museum, London; Sedgwick Museum, Cambridge) there are numerous decalcified bryozoans, typically fenestrates, collected from North Wales. Locality information is often minimal, for example 'Bala Beds'. Many of these specimens were collected early this century and the material is often of little palaeontological value.

Ordovician bryozoans from Britain were first examined in the mid-nineteenth century when they were identified as corals (e.g. M'Coy 1850; Milne-Edwards and Haime 1854). Many of these early descriptions are scanty, with poor illustrations, often showing no internal morphology. Nicholson and Etheridge (1877) and Nicholson (1879) began to include detailed diagrams of sections of specimens showing internal features.

No major monographic study of British Ordovician bryozoans has been completed and only a few papers dealing with small aspects of the fauna have been published. Spjeldnaes (1957) re-

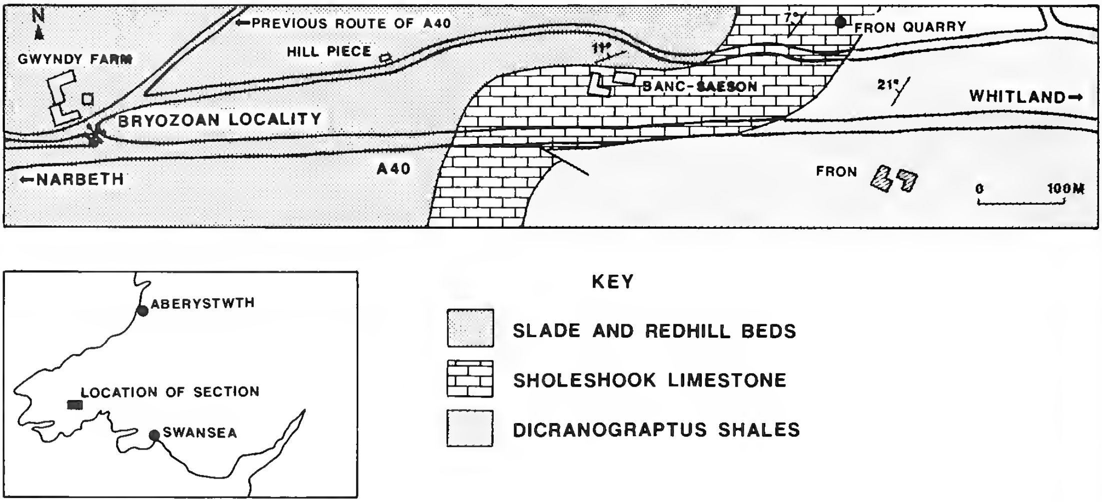
[Palaeontology, Vol. 34, Part 1, 1991, pp. 77–108. 7 pls.]

described some type specimens of British species and later examined some silicified specimens from the Llandeilo of South Wales (Spjeldnaes 1963).

Ross, in three papers (1962, 1963, 1965), examined some of the Caradoc (Cautleyan) bryozoans of Shropshire. This is the most extensive study of an Ordovician bryozoan fauna from Britain to date. Eight species were described from three localities. The fauna includes seven trepostomes and one cryptostome.

There are a few papers describing just one Ordovician species or genus (e.g. Etheridge 1879; Shrubsole 1885). The latest of these is by Taylor and Cope (1987), who describe a specimen of the trepostome genus *Orbipora* from the Lower Arenig of South Wales, noteworthy because it is the oldest bryozoan described in the literature.

Virtually no palaeoecological work has been done on British Ordovician bryozoans. One exception is a study by McNamara (1978) on the symbiosis between gastropods and trepostomes in the Coniston Limestone Group of Cumbria. Detailed systematic descriptions are essential before more interpretive studies can be undertaken on the British fauna.



TEXT-FIG. 1. Map showing the bryozoan locality in the Slade and Redhill Beds near Whitland, Dyfed.

MATERIAL

All study material was collected recently from the Slade and Redhill Beds (upper Rawtheyan, Ashgill), west of Whitland, Dyfed (National Grid Reference SN 164170). The outcrop is a long road section (800 m), revealed during the construction of a new route for the A40 trunk road at Pengawse Hill, exposing horizons from the Dicranograptus Shales (Caradoc) in the east, through the Sholeshook Limestone (lower Ashgill), to the Slade and Redhill Beds in the west (Text-fig. 1). The majority of bryozoans were confined to a 0·3 m thick band composed almost entirely of trepostome bryozoans in a matrix of argillaceous limestone. Crinoid fragments, trilobites (e.g. *Stenopareia* sp. and *Tretaspis* sp.), bivalves, cephalopods and brachiopods (e.g. *Leptaena* sp.) were also found.

The majority of specimens examined from Pengawse Hill were calcified, although many of the bryozoans at or near the surface of the outcrop were partially or totally decalcified. Silicification is seen to occur in some of the calcified colonies. This process can destroy the microstructure, but in the majority of affected colonies the silicification is not too advanced. In tangential sections of some colonies a clear ring of silica can be seen around the zooecial apertures, replacing the bryozoan calcite which forms the zooecial linings (Pl. 3, fig. 7).

The bryozoan fauna at Pengawse Hill is very diverse by British standards. A total of fifteen species has been identified, three of which are new. Four orders are represented: Trepostomata, Cystoporata, Fenestrata and Cyclostomata. Trepostomes dominate with ten species. Fourteen bryozoan species are described in detail in the present work; the cyclostome *Kukersella borealis* (Bassler) is described fully elsewhere (Buttler 1989) and only a brief description is given here.

SYSTEMATIC PALAEONTOLOGY

The terminology used in all descriptions is that of Boardman *et al.* (1983). All genera are placed in families based on the following sources: trepostomes – Astrova (1978); cystoporates – Utgaard (*in* Boardman *et al.* 1983); and phylloporinids – Lavrentjeva (1985). Classification of Palaeozoic trepostome and fenestrate bryozoans at family level is generally unsatisfactory and is currently being revised for the *Treatise on invertebrate paleontology*.

Not all taxa can be identified to species level due to poor preservation or lack of material. In these cases, the species are left in open nomenclature and are referred to as 'cf.' or 'sp.', as recommended by Bengtson (1988).

Biometric details for each trepostome species are tabulated (Table 1). Each measurement was made up to seven times per specimen. The range and mean are calculated for each parameter. All the raw data and further statistical details can be found in an unpublished Ph.D. thesis (Buttler 1988). All specimens described are thin sections/acetate peels unless otherwise stated.

Repository abbreviations: BMNH, Natural History Museum, London; SM, Sedgwick Museum, Cambridge; BGS, British Geological Survey, Keyworth; NMW, National Museum of Wales, Cardiff.

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order TREPOSTOMATA Ulrich, 1882
Suborder HALLOPOROIDEA Astrova, 1965
Family HETEROTRYPIDAE Ulrich, 1890
Genus HETEROTRYPA Nicholson, 1879

Heterotrypa sladei sp. nov.

Plate 1, figs 1–5; Text-fig. 2A

Holotype. BMNH PD8167, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Paratypes. BMNH PD8168–70, from the same horizon and locality as holotype.

Etymology. The species is named after the type horizon.

Diagnosis. Colony ramose. Zooecia parallel branch axis in endozone, curving gradually outwards in exozone. Endozonal walls thin and slightly wavy. Autozooecia rounded-polygonal in transverse section; rounded, occasionally very slightly petaloid in shallow tangential sections. Polygonal mesozooecia present, originating throughout colony. Diaphragms present along entire length of autozooecia, common in exozone; very abundant in mesozooecia, constricting walls and producing a slightly beaded appearance. Acanthostyles small and common throughout colony.

Description. Zoaria erect with cylindrical branches, on average 7·5 mm in diameter. Autozooecia are parallel to branch axis in the inner endozone and gradually curve outwards to meet the zoarial surface at 90°. The autozooecia within the endozone have thin, slightly wavy walls. The exozone has an average diameter of 1·26 mm, and is recognized by a slight thickening of the zooecial walls. Autozooecia all originate in the endozone where they are rounded-polygonal in transverse section. They become rounded and occasionally slightly petaloid in the exozone, as seen in tangential sections of branches. Autozooecial diameters average 0·23 mm by 0·27 mm in the exozone. Thin, orally deflected basal diaphragms are found along the entire length of the colony, spaced 0·32 mm apart in the endozone and becoming more abundant in the exozone where they are spaced 0·13 mm apart. In the outer endozone and exozone occasional cystiphragms are found.

Mesozooecia are present and originate throughout the colony. In the endozone they are polygonal in transverse section and become polygonal-rounded in the exozone, as seen in shallow tangential sections. The maximum diameter of the mesozooecia averages 0·11 mm in the exozone. They contain abundant orally deflected diaphragms, spaced on average 0·18 mm apart in the endozone and 0·1 mm apart in the exozone. Mesozooecial walls are sometimes constricted at the position of the diaphragms, producing a slightly beaded appearance.

Acanthostyles are common and are small with an average diameter of 0·04 mm and density of 9 mm^{-2}. They originate throughout the colony, some are confined to the autozooecial walls but others indent the zooecial apertures, producing a slight petaloid effect. The acanthostyles are composed of a hyaline core surrounded by steeply dipping laminae.

Autozooecial walls are thin and average 0·4 mm in thickness in the exozone. Wall microstructure is composed of steeply inclined, U-shaped laminae. The zooecial wall boundaries are granular and indistinct.

In one specimen (PD8169) there is a layer of thick exozonal type wall within the middle endozone. This type of feature has been regarded as evidence of an abandoned growing tip (Boardman 1960).

Remarks. This is the first species of *Heterotrypa* described from Great Britain. *Heterotrypa sladei* sp. nov. is characterized by very abundant diaphragms throughout the zoarium, beaded mesozooecia, thin endozonal walls and small acanthostyles common throughout the colony. It is unusual for the genus in having abundant diaphragms within the endozone. Boardman and Utgaard (1966, p. 1105) in their revision of *Heterotrypa* state that diaphragms within the endozone are rare to moderately abundant.

H. sladei is similar to *H. frondosa* (d'Orbigny, 1850) illustrated by Boardman and Utgaard (1966, pl. 140), although diaphragms are more abundant in the endozone of the new species. *H. magnopora* Boulange, 1963 was described from the Montagne Noire (upper Ordovician) and has a similar exozone to *H. sladei* but differs in having sparse acanthostyles in the endozone.

Genus DEKAYIA Milne-Edwards and Haime, 1851

Dekayia pengawsensis sp. nov.

Plate 1, figs 6–8; Plate 2, fig. 1; Text-fig. 2B.

Holotype. BMNH PD8176, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Paratypes. BMNH PD8178–9, from the same horizon and locality as holotype.

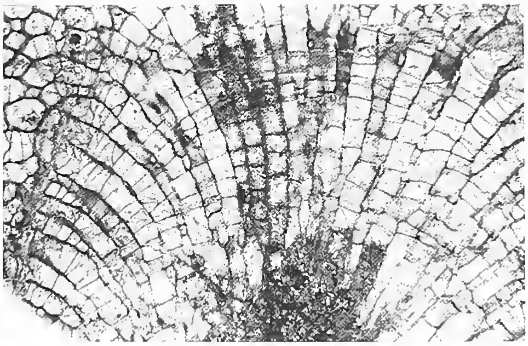
Etymology. The species is named after the type locality.

EXPLANATION OF PLATE 1

Figs 1–5. *Heterotrypa sladei* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8167 (paratype), longitudinal section, × 15. 2, BMNH PD8167 (holotype), longitudinal section, × 28. 3, BMNH PD8170 (paratype), longitudinal section, showing layer of thicker exozonal material within the endozone, × 48. 4, BMNH PD8169 (paratype), tangential section, × 48. 5, BMNH PD8169 (paratype), tangential section, showing an acanthostyle inflecting an autozooecium, × 120.

Figs 6–8. *Dekayia pengawsensis* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 6, BMNH PD8179 (paratype), longitudinal section, × 15. 7, BMNH PD8179 (paratype), longitudinal section, showing large acanthostyles in endozone, × 28. 8, BMNH PD8176 (holotype), tangential section, × 48.

PLATE 1



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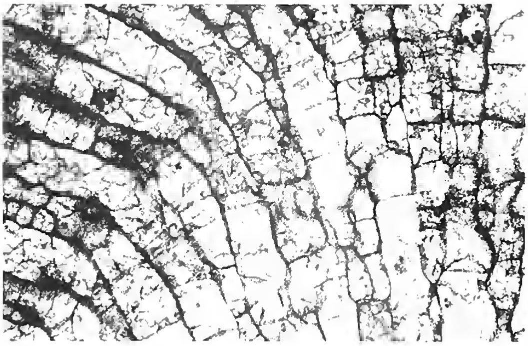

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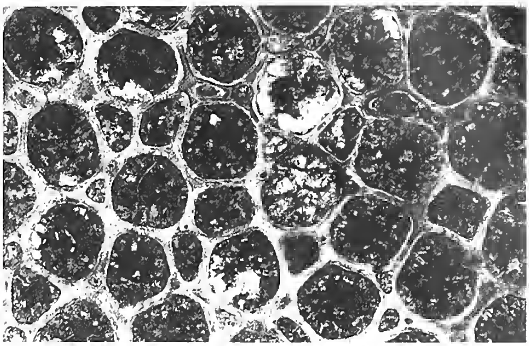

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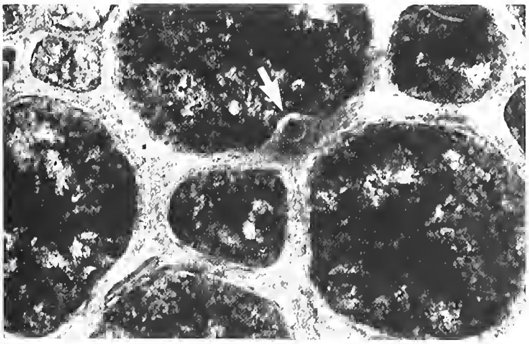

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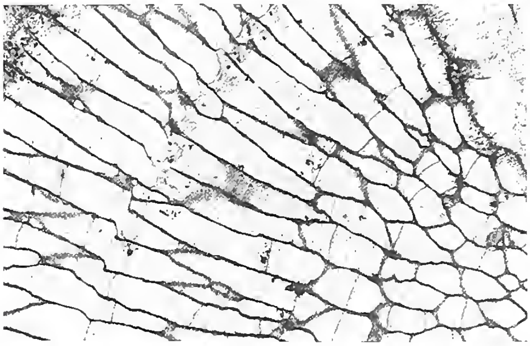

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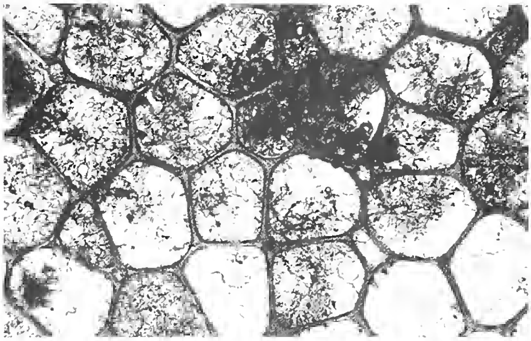

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BUTTLER, *Heterotrypa*, *Dekayia*

Diagnosis. Colony hemispherical. Zooecia originate from the basal lamina. Zooecial walls wavy, slightly thickened in exozone. Autozooecia polygonal to polygonal-rounded in transverse section throughout colony. Polygonal mesozooecia uncommon. Diaphragms present in all zooecia. Acanthostyles abundant throughout colony.

Description. Zoaria are hemispherical with an average diameter of 11 mm. Autozooecia all originate at the centre of the colony and curve outwards towards the zoarial surface. Autozooecial walls are slightly wavy throughout the colony. Endozone:exozone boundary indistinct. Autozooecia are large, with an average diameter of 0·29 mm by 0·32 mm, and are polygonal to polygonal-rounded in transverse section throughout the colony. Thin diaphragms are present, though not abundant, in all zooecia, and are spaced between 0·13 mm and 0·86 mm apart, with an average of 0·48 mm. They increase in frequency slightly at the periphery of the colony. These basal diaphragms are all deflected orally at their junctions with the zooecial walls and their laminae are continuous with the autozooecial linings.

Mesozooecia are present but not common. They are polygonal in transverse section and have an average maximum diameter of 0.12 mm. Mesozooecia contain orally deflected basal diaphragms, spaced on average 0·11 mm apart in the exozone.

Acanthostyles are abundant and originate throughout the colony. They are composed of a large hyaline core surrounded by steeply dipping laminae.

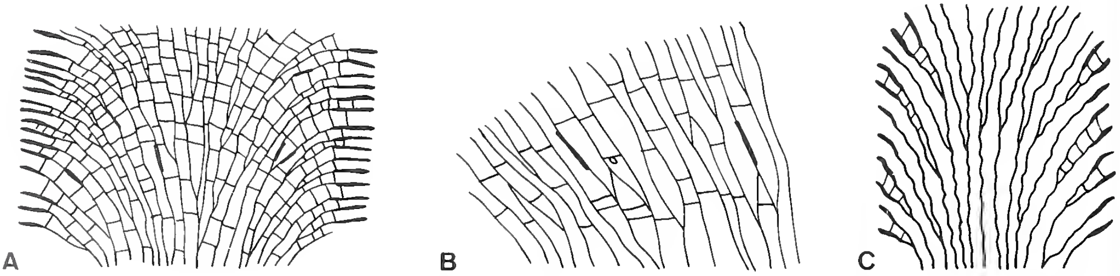
Autozooecial wall thickness averages 0·02 mm in the exozone. Wall microstructure is composed of inclined U-shaped laminae. Zooecial boundaries are distinguished by a darker granular zone in the centre of the walls.

In one specimen (PD8176) hollow 'cyst' structures are found within the autozooecia. These are spherical, average 0·03 mm in diameter, and occur singularly or in pairs. The 'cysts' are attached to the sides of the zooecial walls and their laminae are continuous with the zooecial linings.

Two of the specimens (PD8176, 8178) use colonies of *Leioclema orbicularis* as substrata for encrustation. In all of the colonies, periods of growth cessation can be inferred by the presence of a row of thick basal diaphragms followed by a change in the orientation of the zooecia.

Remarks. *Dekayia pengawsensis* sp. nov. is primarily characterized by the hemispherical form, the thin wavy zooecial walls and the rare mesozooecia. Diaphragms are present and acanthostyles are abundant throughout the colony. Prior to this study the genus *Dekayia* had not been recorded in Britain.

D. pengawsensis is similar internally to the ramose *D. aspera* Milne-Edwards and Haime, 1851, which was well illustrated by Boardman and Utgaard (1966, pl. 138). The Welsh specimens, however, have smaller acanthostyles and more abundant diaphragms. *D. semipilans* (Ulrich, 1890), figured by Brown and Daly (1986, pl. 4, figs 9–12), has a similar wall structure and acanthostyles to *D. pengawsensis* but again lacks diaphragms. *D* cf. *crenulata* Prantl, 1940 has been found from the same locality. This differs from *D. pengawsensis* by the ramose colony form, the beaded mesozooecia and the greater abundance of acanthostyles.



TEXT-FIG. 2. Longitudinal sketch sections of new species of bryozoans described from the Slade and Redhill Beds. A, *Heterotrypa sladei*. B, *Dekayia pengawsensis*. C, *Anaphragma gwyndyense*.

Dekayia cf. *crenulata* Prantl, 1940

Plate 2, figs 2–4

Material. BMNH PD8171–3, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, W of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with cylindrical branches, on average 7 mm in diameter. The surfaces of all specimens are slightly abraded. Autozooecia are generally parallel to the branch axis in the endozone and they gradually curve outwards and meet the zoarial surface at 90°. The autozooecia within the endozone have quite thin crenulated walls. The exozone is relatively narrow with an average diameter of 0·06 mm. It is recognized by a slight thickening of the zooecial walls and a change in the zooecial orientation, which occur simultaneously. Autozooecia all originate in the endozone where they are polygonal-rounded in transverse section. They become rounded in the exozone as seen in tangential sections of branches. Autozooecial diameters average 0·22 mm by 0·27 mm. Diaphragms are absent in the endozone but are occasionally present within the autozooecia in the exozone where they are spaced on average 0·25 mm apart. These diaphragms are all deflected orally at their junctions with the zooecial walls and their laminae are continuous within the autozooecial linings.

Mesozooecia are present but uncommon, and originate in the outer parts of the endozone and inner parts of the exozone. They are rounded-polygonal in shape, as seen in shallow tangential sections, and have a maximum diameter of 0·12 mm. The mesozooecia contain orally deflected basal diaphragms, spaced on average 0·15 mm apart in the endozone and 0·13 mm in the exozone. Mesozooecial walls often have a beaded appearance in longitudinal section. In the exozone this is caused by the zooecial walls constricting slightly at the position of the diaphragms. In the endozone the mesozooecial walls appear to pinch together, producing a similar beaded appearance.

Acanthostyles are very abundant, with an average diameter of 0·05 mm and density of 7 mm^{-2} the exozone. They are large and long, originate randomly throughout the colony, and may indent autozooecial walls. Acanthostyles all have a wide hyaline core, surrounded by steeply dipping conical laminae.

Autozooecial wall thickness averages 0·03 mm in the exozone. Wall microstructure is composed of inclined, U-shaped laminae, with indistinct zooecial boundaries. Some zooecia are infilled with laminar calcite close to the colony surface. In longitudinal section this infilling consists of very broad U-shaped laminae.

Remarks. The specimens described herein are distinguished by the thin crenulated walls in the endozone, the rare mesozooecia and the large abundant acanthostyles throughout the colony.

Prantl (1940) described the Ashgillian species *Dekayia crenulata* from east of Grange du Pin, Herault, Montagne Noire, France. This species has slender branches, an absence of mesozooecia, crenulated autozooecial walls in the axial region of the zoarium and numerous acanthostyles throughout the colony. The walls and acanthostyles are similar in specimens from Wales and the Montagne Noire. The autozooecial apertures of *D. crenulata* described by Prantl are generally smaller than those of the specimens from Wales (0·17–0·21 mm Montagne Noire; 0·19–0·32 mm Wales); however, the ranges overlap. The size of the colonies also varies: *D. crenulata* has a branch diameter of 3·6–4·6 mm, the Welsh specimens are larger at 7–8 mm. Mesozooecia are stated as absent in *D. crenulata* by Prantl. In the Welsh specimen PD 8173 they are present but they are very rare in specimen PD 8172. This may reflect within species variability. For the present, until further material can be examined, the specimens are assigned to *D.* cf. *crenulata.*

Genus LEIOCLEMA Ulrich, 1882

Leioclema orbicularis Modzalevskaya, 1953

Plate 2, figs 5–8; Plate 3, figs 1 and 2

1921 *Leioclema spineum ramosum* Bekker, p. 41, pl. 6, figs 14–18.
1953 *Leioclema spineum* Ulrich var. *orbicularis* Modzalevskaya, p. 147, pl. 9, figs 4–6; text-fig. 23.

Material. BMNH PD8159–8164, 8166*a*, *b*; Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. ?Kuckers Stage (middle Ordovician), NE Estonia, USSR. Middle Ordovician, Leningrad Oblast'. USSR (Modzalevskaya 1953).

Description. Zoaria erect with cylindrical branches, on average 6·4 mm in diameter. Autozooecia are roughly parallel to the branch axis within the endozone and gradually curve outwards to meet the zoarial surface at 70°–90°. Autozooecial walls are thin within the endozone and slightly wavy. The exozone has an average diameter of 1·66 mm, and is recognized by a thickening of the zooecial walls. Autozooecia originate within the endozone, where they are polygonal-rounded in transverse section. They become rounded-petaloid in the exozone, as seen in tangential sections of branches. Autozooecial diameters in the exozone average 0·25 mm by 0·34 mm. Diaphragms are rare and often absent. If present, there are usually only one or two per autozooecium and they are located in the exozone.

Mesozooecia are common, originate within the endozone and have an average maximum diameter of 0·16 mm. In shallow tangential sections they are polygonal-rounded in shape. Mesozooecia contain abundant orally deflected basal diaphragms, spaced on average 0·15 mm apart in the endozone and 0·08 mm in the exozone, with successive diaphragms generally increasing in thickness distally along the mesozooecium.

Acanthostyles are large and abundant, with an average diameter of 0·1 mm and density of 8 mm^{-2}. They can occur throughout the exozone and they frequently indent the autozooecial apertures to produce a petaloid shape. A hyaline calcite core is surrounded by steeply dipping conical laminae.

Autozooecial wall thickness averages 0·12 mm in the exozone. Microstructure is difficult to distinguish because the walls are considerably disrupted by the presence of the large acanthostyles; however, walls can be seen to be composed of steeply inclined, U-shaped laminae. Diaphragms in the distal exozone are continuous with the zooecial wall laminae. Some of the zooecia, especially mesozooecia, become infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Remarks. This species is characterized by an erect colony form, and thin autozooecial walls in the endozone which become thickened in the exozone. Autozooecial apertures are rounded-petaloid in shallow tangential section. Diaphragms are rare in autozooecia but common in mesozooecia. Acanthostyles are large and abundant in the exozone.

Leioclema spineum Ulrich var. *orbicularis* Modzalevskaya, 1953 was first described from the middle Ordovician of Leningrad Oblast' and Estonia. The *L. spineum* Ulrich as described by Bassler (1911) was characterized by a ramose colony form, numerous diaphragms in the abundant mesozooecia and occasional ones in the autozooecia, and exceedingly large acanthostyles. *L. spineum orbicularis* differs from *L. spineum* in having more abundant smaller acanthostyles and fewer mesozooecia. This internal structure is similar to *Leioclemella clava* Bassler, 1911. The genus *Leioclemella* is, however, characterized by having a club-shaped zoarium seemingly jointed at the base. Articulation is unknown in trepostomes and this feature may instead be a paraboloid base of the sort described by McKinney (1977). The differences between *L. spineum orbicularis* and *L. spineum* are herein considered to be significant enough to raise the subspecies *L. spineum orbicularis* to species rank.

The specimens described here are very similar to *L. orbicularis* from the USSR. Although the acanthostyles of the Welsh material are larger than those shown in Modzalevskaya (1953, text-fig. 23), her tangential sections are deeper than those of the Welsh material.

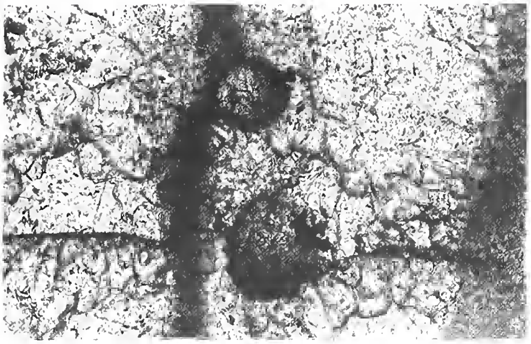
EXPLANATION OF PLATE 2

Fig. 1. *Dekayia pengawsensis* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, BMNH PD8176 (holotype), longitudinal section, showing 'cyst' structures, × 120.

Figs 2–4. *Dekayia* cf. *crenulata* Prantl, 1940. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 2, BMNH PD8172, longitudinal section, × 28. 3, BMNH PD8173, longitudinal section, × 28. 4, BMNH PD8172, tangential section, showing acanthostyles, × 38.

Figs 5–8. *Leioclema orbicularis* Modzalevskaya, 1953. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 5, BMNH PD8161, longitudinal section, × 15. 6, BMNH PD8161, longitudinal section, showing the endozone, × 28. 7, BMNH PD8161, longitudinal section, showing large acanthostyles in the exozone, × 55. 8, BMNH PD8161, transverse section, × 28.

PLATE 2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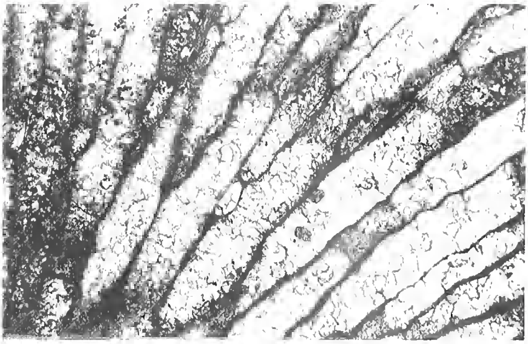
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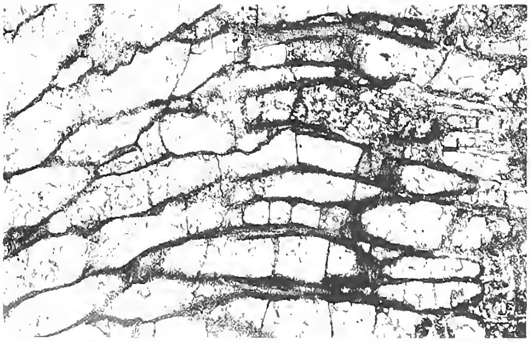
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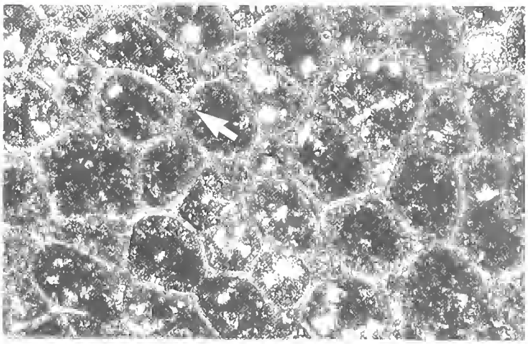
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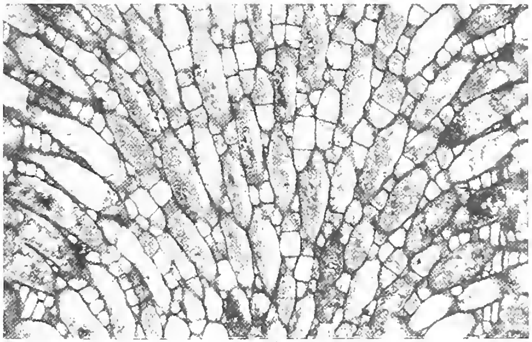
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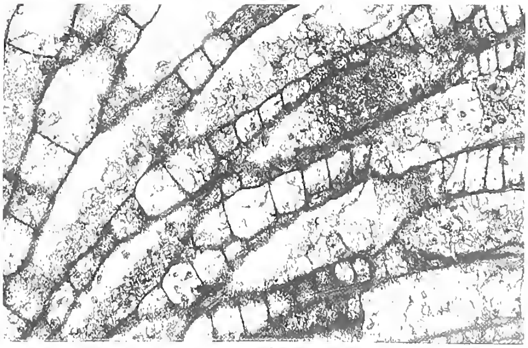
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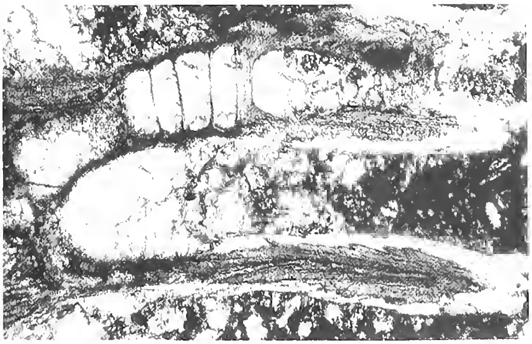
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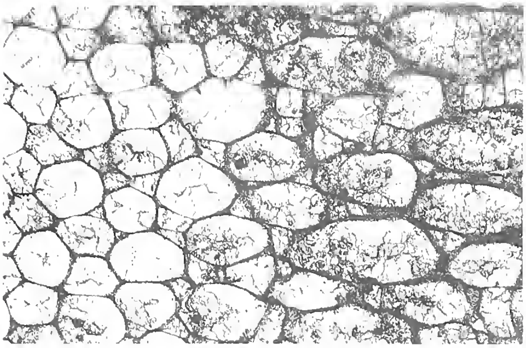
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BUTTLER, *Dekayia*, *Leioclema*

Bekker (1921) described the variety *L. spineum ramosum* from the Kuckers Stage (middle Ordovician) of NE Estonia, which he regarded as an intermediate form between *L. spineum* and *Leioclemella clava*. Bekker explained 'The acanthostyles of my specimen agree much more with those of *Leioclemella*, but the habit of growth (*Leioclemella clava* – clubshaped) separates them'. This would suggest that *L. spineum ramosum* is an erect ramose form, but Bekker's plate (1921, pl. 6, fig. 18) shows the cone-shaped origin of the colony suggesting a possible paraboloid base like that of *Leioclemella*. The illustrations are, however, poor and the type material (housed in the Geological Museum at the University of Tartu, Estonia) would have to be examined for a positive identification, pending which this species is tentatively placed within *L. orbicularis*.

Family HALLOPORIDAE Bassler, 1911

Genus HALLOPORA Bassler, 1911

Hallopora peculiaris Pushkin (*in* Ropot and Pushkin, 1987)

Plate 3, figs 3–8

1987 *Hallopora wesenbergiana peculiaris* Pushkin *in* Ropot and Pushkin; p. 153, pl. 8, fig. 5; pl. 9, fig. 1.

Material. BMNH PD8237–82, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170)

Other occurrence. Piriguskii Stage (lower Ashgill), Shikipi, Latvia, USSR (Pushkin *in* Ropot and Pushkin 1987).

Description. Zoaria erect with cylindrical branches on average 8·3 mm in diameter. Autozooecia curve gradually away from the branch axis in the endozone and meet the zoarial surface at approximately 80–90°. In the endozone the zooecial walls are very thin. The exozone, recognized by a thickening of the zooecial walls, has an average width of 1·65 mm. Autozooecia are circular in transverse section throughout the colony and average 0·37 mm in diameter in the exozone. There is an average of 5 autozooecia mm^{-2} in the exozone. Diaphragms are rare within the autozooecia and when present, usually occur closely spaced in the distal exozone. These basal diaphragms are deflected orally at their junctions with the zooecial walls and their laminae are generally continuous with the zooecial linings. The average spacing between the diaphragms is 0·16 mm in the endozone and 0·15 mm in the exozone.

Mesozooecia are common throughout the whole zoarium, often originating in the inner parts of the endozone. Mesozooecial walls are thin in the endozone and thicken in the exozone. They are polygonal to polygonal-rounded in shallow tangential sections, with an average maximum diameter of 0·16 mm in the exozone. Basal diaphragms are present throughout their length, spaced on average 0·13 mm apart in the endozone and 0·07 mm in the exozone. Diaphragms tend to increase in thickness distally along the mesozooecia. In some colonies mesozooecial walls are constricted at the position of the diaphragms, producing a slightly beaded appearance.

Autozooecial wall thickness averages 0·08 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae. The precise contact between the zooecia is indistinct. The thickened exozonal

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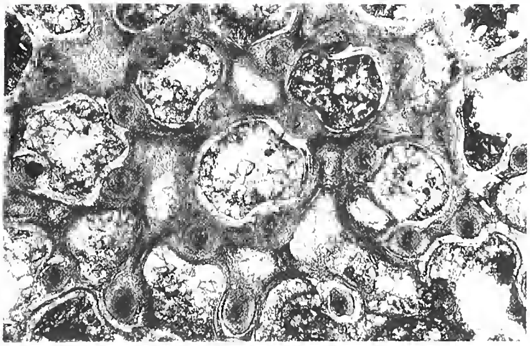
EXPLANATION OF PLATE 3

Figs 1 and 2. *Leioclema orbicularis* Modzalevskaya, 1953. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8161, tangential section, × 35. 2, BMNH PD8161, tangential section, showing large acanthostyles, × 80.

Figs 3–8. *Hallopora peculiaris* Pushkin (*in* Ropot and Pushkin, 1987). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 3, BMNH PD8278, longitudinal section, × 28. BMNH PD8282, longitudinal section, × 28. 5, BMNH PD8278, transverse section, × 28. 6, BMNH PD8278, longitudinal section, showing the V-shaped microstructure, × 75. 7, BMNH PD8278, tangential section, showing rings of clear silica replacing the autozooecial linings, × 40. 8, BMNH PD8257, tangential section, showing maculae composed predominantly of mesozooecia, × 28.

PLATE 3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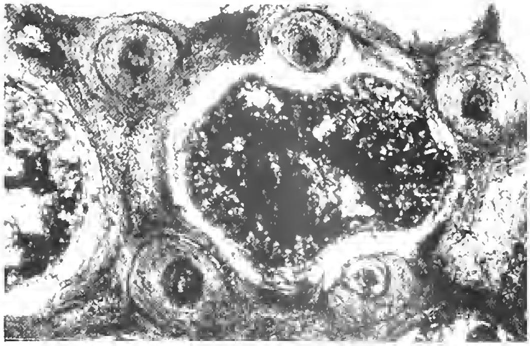
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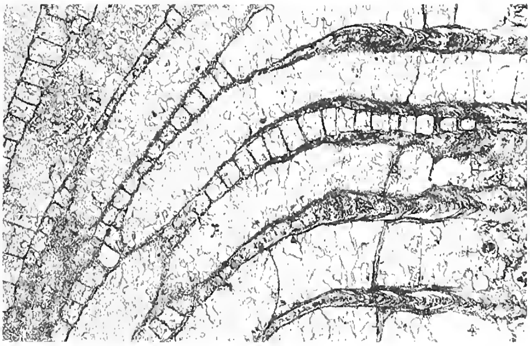
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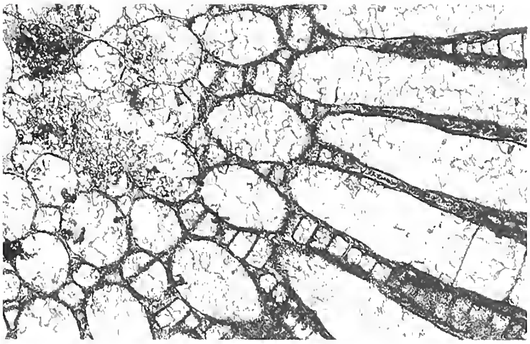
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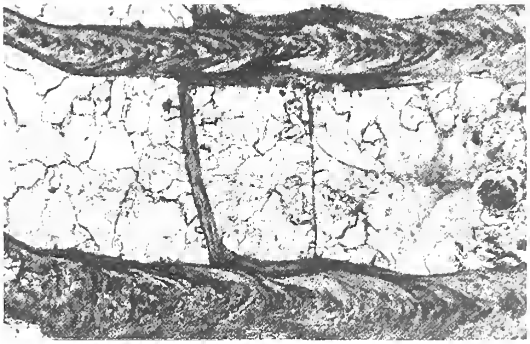
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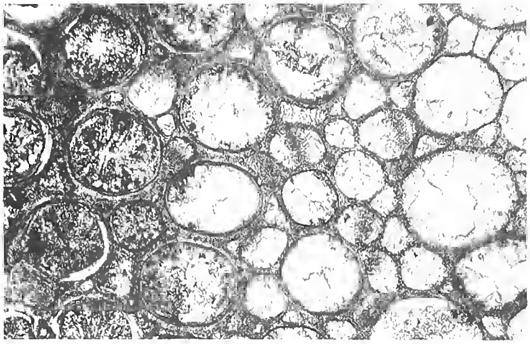
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BUTTLER, *Leioclema*, *Hallopora*

diaphragms in the mesozooecia are also laminar and are continuous with the wall laminae. Some zooecia, especially mesozooecia, are infilled with laminar calcite close to the zoarial surface. In longitudinal sections this infilling consists of broad U-shaped laminae.

Maculae composed of a concentration of mesozooecia have been recognized in thin sections (Pl. 3, fig. 8).

Overgrowths are present in several colonies (e.g. PD8237). These are composed of endozonal and exozonal elements, and often contain abundant diaphragms.

Remarks. Hallopora peculiaris is primarily characterized by the extensive beaded mesozooecia which originate in the inner endozone. The autozooecia are circular throughout the colony, and diaphragms are rare in the endozone, becoming more abundant in the outermost regions.

Pushkin (*in* Ropot and Pushkin, 1987) created a new sub-species *H. wesenbergiana peculiaris*, which differed from the Estonian *H. wesenbergiana* (Dybowski) by the absence of diaphragms within the endozonal autozooecia. The mesozooecia in *H. wesenbergiana* are less prominent than in *H. wesenbergiana peculiaris* and are not beaded. The differences are considered significant to raise *H. wesenbergiana peculiaris* to species rank.

One other species of *Hallopora* is here described from Pengawse Hill, *H.* cf. *elegantula*, a very slender form, with large and abundant mesozooecia.

Hallopora peculiaris is similar to *H. solbergiensis* described from the upper Ordovician *Dalmanitina* beds of Borenshult, Ostergötland, Sweden by Brood (1978). The Swedish species, however, differs from the Welsh by its smaller size (colony branches 3–5 mm wide), the more abundant diaphragms within the autozooecia, and the relatively greater size of the mesozooecia.

Hallopora cf. *elegantula* (Hall, 1852)

Plate 4, figs 1 and 2

Material. BMNH PD8180–82, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with slender cylindrical branches, on average 3·2 mm in diameter. Autozooecia curve outwards from the branch axis to meet the colony surface at 90°. The autozooecia within the endozone have thin walls. The exozone is narrow with an average width of 0·86 mm and is recognizable by a slight thickening of the zooecial walls.

Autozooecia are circular in section throughout the colony and average 0·26 mm by 0·31 mm in diameter in the exozone. Diaphragms are found along the whole length of the autozooecia, but are rare in the exozone. They are spaced on average 0·17 mm apart in the endozone.

Mesozooecia are common, originate within the endozone and have an average maximum diameter of 0·15 mm. In shallow tangential section the polygonal mesozooecia are seen to fill in the spaces between the circular autozooecia. Mesozooecia contain orally deflected diaphragms throughout their length which are spaced on average 0·1 mm apart in the endozone and 0·05 mm in the exozone, increasing in abundance distally along each mesozooecium.

EXPLANATION OF PLATE 4

Figs 1 and 2. *Hallopora* cf. *elegantula* (Hall, 1852). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8181, longitudinal section, ×38. 2, BMNH PD8181, transverse section, ×48.

Figs 3–6. ?*Batostoma* sp. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 3, BMNH PD8332, longitudinal section, ×32. 4, BMNH PD8332, longitudinal section, showing large acanthostyles which lack sheathing laminae, ×60. 5, BMNH PD8236*d*, transverse section, showing the irregularly shaped autozooecia within the endozone, ×28. 6, BMNH PD8236*d*, tangential section, ×48.

Figs 7–8. *Eridotrypa* sp. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 7, BMNH PD8319*a*, longitudinal section, ×38. 8, BMNH PD8319*a*, tangential section, showing small acanthostyle-like structures, ×105.

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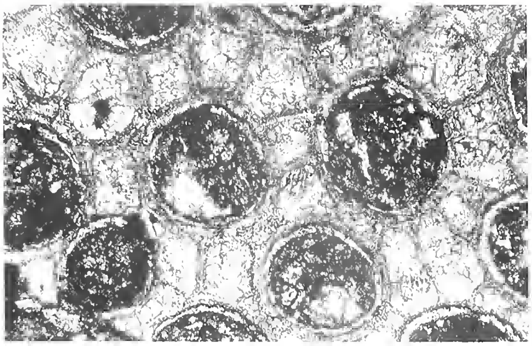

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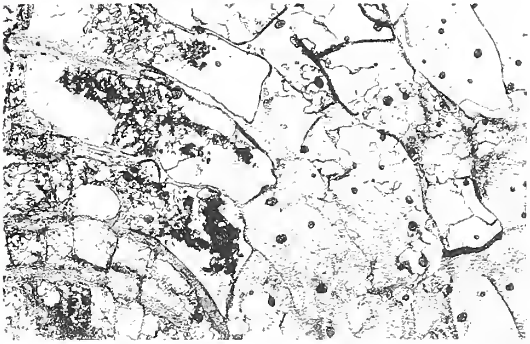

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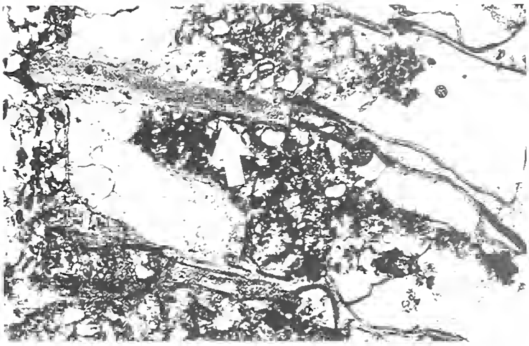

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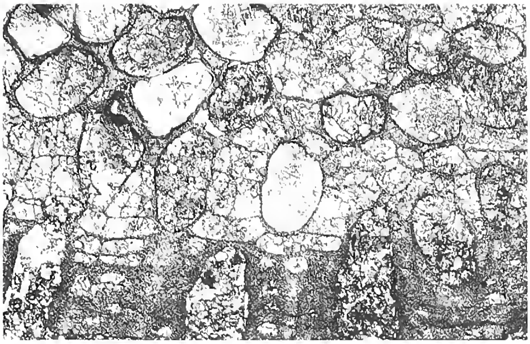

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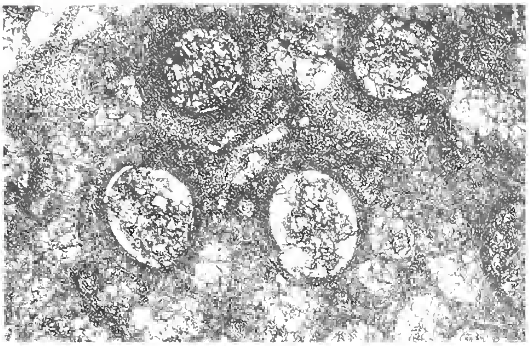

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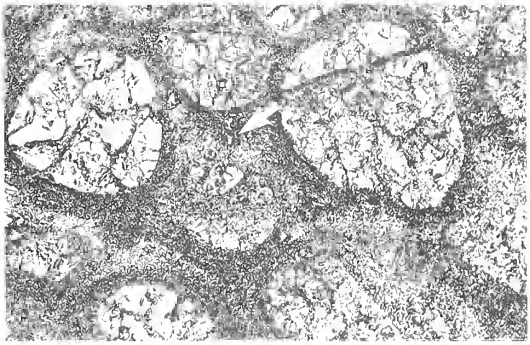

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BUTTLER, *Hallopora*, ?*Batostoma*, *Eridotrypa*

Autozooecial wall thickness averages 0·1 mm in the exozone. Wall microstructure is composed of inclined, U-shaped laminae. Zooecial boundaries are indistinct.

Remarks. This species is only known from randomly oriented peels of poorly preserved specimens. It is characterized by the narrow colony branches and thin-walled autozooecia curving out gradually from the branch axis. Autozooecia are circular in cross section throughout the colony. Polygonal mesozooecia are common and surround the autozooecia. Diaphragms are present in the autozooecia and very abundant in the mesozooecia.

Internally, the specimens are very similar to *Hallopora elegantula* Hall, an Ordovician and Silurian species with an extensive distribution. They have similar polygonal mesozooecia surrounding the autozooecia, and similar diaphragms. *H. elegantula* is, however, characterized by ornamented, perforated terminal diaphragms found usually at the outer ends of the autozooecia but also within the exozone (Conti and Serpagli 1987). As these have not been observed in the Welsh specimens, this material is therefore identified as *H.* cf. *elegantula.*

Family TREMATOPORIDAE Miller, 1889
Genus BATOSTOMA Ulrich, 1882

?*Batostoma* sp.

Plate 4, figs 3–6

Material. BMNH PD8332, 8236*d*, 8319*b*, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with cylindrical branches, on average 5·3 mm in diameter.

Autozooecia appear to curve out from the branch axis to meet the zoarial surface at 70°. The autozooecia within the endozone have very thin wavy walls.

The exozone has an average width of 1·37 mm. It is recognized both by a slight thickening of the zooecial walls and a change in zooecial orientation.

Autozooecia all originate in the endozone where they are irregular-polygonal in transverse section, becoming circular in the exozone as seen in tangential sections of branches. Autozooecial diameters average 0·26 mm by 0·31 mm within the exozone. Diaphragms are present in autozooecia in the exozone and may also occur in the endozone but are hard to distinguish here owing to the poor preservation. These basal diaphragms are all deflected orally at their junctions with zooecial walls and their laminae are continuous with the autozooecial linings.

Mesozooecia are present and originate in the endozone. They are polygonal in shallow tangential section and have an average maximum diameter of 0·12 mm. They contain orally deflected basal diaphragms in the exozone, spaced on average 0·2 mm apart and often slightly increasing in thickness distally along the mesozooecium.

Acanthostyles are very large and abundant, with an average diameter of 0·06 mm and a density of 10 mm^{-2}. They originate deep in the exozone, occasionally indent autozooecial apertures, and are composed of a very wide hyaline calcite core without a surrounding sheath of lamellae.

Autozooecial wall thickness averages 0·14 mm in the exozone. Wall microstructure consists of steeply inclined U-shaped laminae and is hard to distinguish because of the presence of the large acanthostyles. Some zooecia, especially mesozooecia, are filled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Remarks. Only three poorly-preserved specimens (two in randomly oriented peels) have been found. This species is very unusual and is characterized by the irregularly polygonal autozooecial apertures, which become circular in shallow tangential sections. Autozooecial walls are very thin and irregular within the endozone and become greatly thickened in the outer exozone. Diaphragms are present in the exozonal autozooecia and are irregularly spaced. Acanthostyles are abundant, large and composed entirely of a hyaline core with no surrounding laminae.

Generic assignment of this species is difficult because of the poor preservation of the specimens. The erect colony, the occurrence of diaphragms in the autozooecia, and the presence of acanthostyles fit the generic concept of *Batostoma*. However, the detailed structure of the acanthostyles and endozonal walls is apparently unique and provides a basis for the suggestion that this material may represent a new genus. The large, simple acanthostyles are similar to those observed in early Ordovician forms such as *Nekhorosheviella* Modzalevskaya. As three poorly preserved specimens do not provide sufficient information to erect a new genus, the assignment is given tentatively as ?*Batostoma* sp.

Genus ERIDOTRYPA Ulrich, 1893

Eridotrypa sp.

Plate 4, figs 7 and 8

Material. BMNH PD8319*a*, 8236*e*, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria erect with very narrow cylindrical branches, on average 1·5 mm in diameter. This species has only been recognized in randomly oriented peels. Autozooecia are parallel to the branch axis within the endozone and then curve slightly in the exozone to meet the zoarial surface at 45°. The autozooecia within the endozone have thin, straight walls. The exozone is narrow with an average diameter of 0·53 mm. It is recognized by a slight thickening of the zooecial walls. Autozooecia all originate in the endozone (though no specimens have been observed in transverse section), and are oval in the exozone, as seen in tangential sections of the branches. Autozooecial diameters average 0·11 mm by 0·15 mm within the exozone. Diaphragms are present throughout the autozooecia and are widely-spaced, on average 0·21 mm apart in the endozone and 0·12 mm in the exozone. These basal diaphragms are all deflected orally at their junctions with zooecial walls.

Small polygonal mesozooecia may be present in the exozone, but are hard to distinguish. Acanthostyle-like structures have been observed in the exozone; their structure cannot be distinguished.

Autozooecial wall thickness averages 0·04 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae, but is, however, indistinct.

Remarks. The specimens of *Eridotrypa* from Pengawse Hill are from randomly orientated peels. They are characterized by a narrow ramose colony form; autozooecial walls are thin and diaphragms are found throughout the colony. Autozooecial apertures are oval in shallow tangential sections; mesozooecia are present.

Suborder AMPLEXOPOROIDEA Astrova, 1965
Family AMPLEXOPOROIDAE Miller, 1889
Genus ANAPHRAGMA Ulrich and Bassler, 1904

Anaphragma dnestrense Astrova, 1965

Plate 5, figs 1–4

1965 *Anaphragma dnestrense* Astrova, p. 235, pl. 56, figs 1*a* and *b*.
1966 *Anaphragma portranense* Ross, p. 111, pl. 1, figs 1, 2, 4, 6; pl. 6, figs 4, 6.

Material. BMNH PD8204–34, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. Molodovskii Stage (upper Ordovician), Podolia, USSR (Astrova 1965). Portrane Limestone (Cautleyan, Ashgill), Portrane, Co. Dublin, Ireland (Ross 1966).

Description. Zoaria erect with cylindrical branches, on average 6·4 mm in diameter. The surfaces of all specimens are abraded. Autozooecia generally parallel the branch axis in the endozone. They then gradually curve outwards to meet the zoarial surface at approximately 80°. Within the endozone the autozooecial walls are thin and crenulated. The exozone, recognized by a slight thickening of the zooecial walls and a change in the orientation of the zooecia, has an average diameter of 1·34 mm. Autozooecia are polygonal in the endozone in transverse section and become rounded in the exozone as seen in tangential sections of branches. Autozooecia average 0·33 mm by 0·43 mm diameter in the exozone. Diaphragms are absent in all of the autozooecia.

Exilazooecia are common and originate in the outer parts of the endozone. They are rounded-polygonal in shape in shallow tangential sections, with a maximum diameter which averages 0·16 mm.

Acanthostyles are abundant, usually small and inconspicuous. Their diameter ranges from 0·01 mm to 0·06 mm. In some acanthostyles a calcite hyaline core has been observed, surrounded by conical calcite laminae.

Autozooecial wall thickness averages 0·08 mm in the exozone. Wall microstructure is composed of steeply inclined, V-shaped laminae. Zooecial boundaries are distinguished by a darker granular zone. Some autozooecia and exilazooecia are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Overgrowths, composed of exozonal elements, have been recognized in a few specimens.

Remarks. *Anaphragma dnestrense* was described from the Molodovskii Stage of Podolia in the Arctic Soviet Union by Astrova (1965) and has hitherto not been recognized elsewhere. *A. portranense* was described by Ross (1966) from the Portrane Limestone in Ireland. It was diagnosed as '*Anaphragma* with slender branches having large zooecial openings, numerous small acanthopores which penetrate the junctions of the zooecial walls and mesopore walls, and numerous mesopores'. *A. dnestrense* is similar in most aspects to *A. portranense*. The colony size of the Welsh material (4–9 mm zoarial diameter) is generally larger than that of *A. portranense* (3 mm); however, the Soviet material has a very wide range of colony size (3–14 mm) spanning the two groups. All other measurements given for the holotype of *A. portranense* (Ross 1966, p. 112) extend into the range measured from the Welsh specimens of *A. dnestrense*. Therefore, *A. portranense* is placed in synonymy with *A. dnestrense*.

A. dnestrense is similar to *A. mirabile* Ulrich and Bassler, 1904 which was redescribed by Boardman (1960). *A. mirabile* has been recognized from the upper Ordovician of North America (Richmondian Group, Illinois and Wisconsin) and Estonia (Lyckholm Limestone, Island of Dago). However, the walls of *A. mirabile* are less crenulated in the endozone, there are fewer exilazooecia, and the exozone is larger in relation to the endozone than in *A. dnestrense*. In the outer exozone of *A. mirabile* the acanthostyles become very large (Boardman 1960, pl. 4, fig. 2), whereas in *A. dnestrense* they remain small.

One other species of *Anaphragma* has been recognized in this study from the same locality (Pengawse Hill, near Whitland). *A. gwyndyense* sp. nov. has thick walls in the endozone, tabulated polymorphs (i.e. mesozooecia) and rare acanthostyles which distinguish it from *A. dnestrense*.

Anaphragma gwyndyense sp. nov.

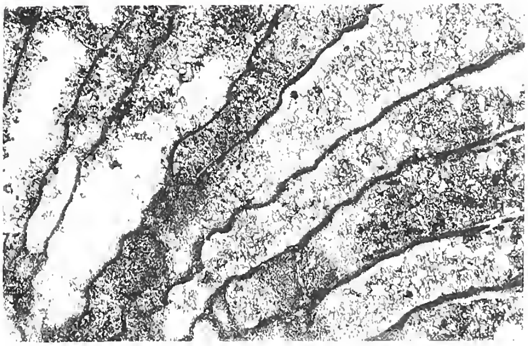
Plate 5, figs 5–8; Text-Fig. 2c

Holotype. BMNH PD8195, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

EXPLANATION OF PLATE 5

Figs 1–4. *Anaphragma dnestrense* Astrova, 1965. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8232, longitudinal section, ×28. 2, BMNH PD8229, longitudinal section, ×28. 3, BMNH PD8235, tangential section, ×38. 4, BMNH PD8235, tangential section, showing small acanthostyles within the walls, ×110.

Figs 5–8. *Anaphragma gwyndyense* sp. nov. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 5, BMNH PD8195 (holotype), longitudinal section, showing the thick crenulated walls within the endozone, ×28. 6, BMNH PD8196 (paratype), longitudinal section, ×48. 7, BMNH PD8195 (holotype), tangential section, ×48. 8, BMNH PD8192 (paratype), tangential section, showing small acanthostyles in the zooecial walls, ×110.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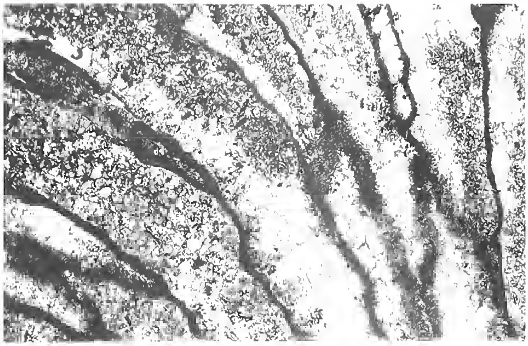
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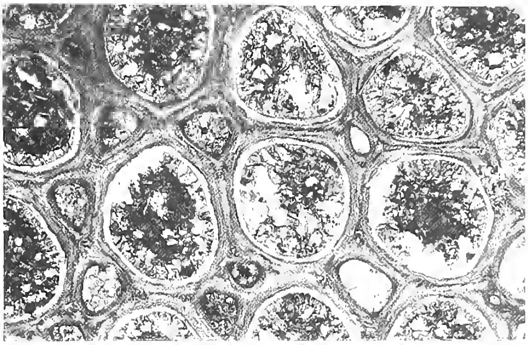
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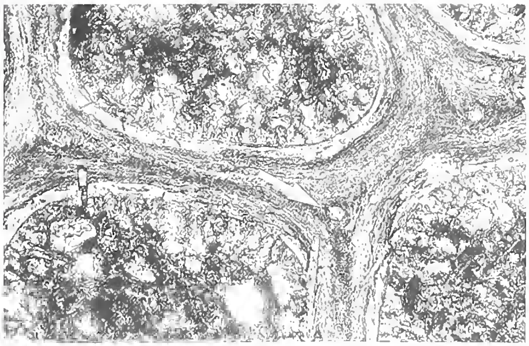
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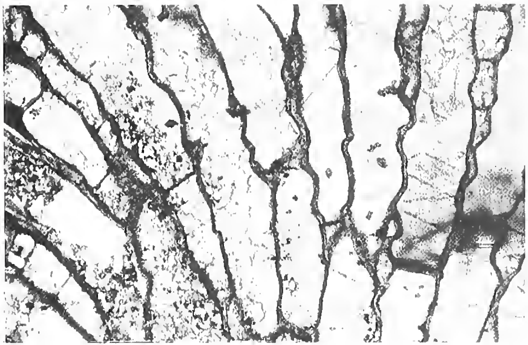
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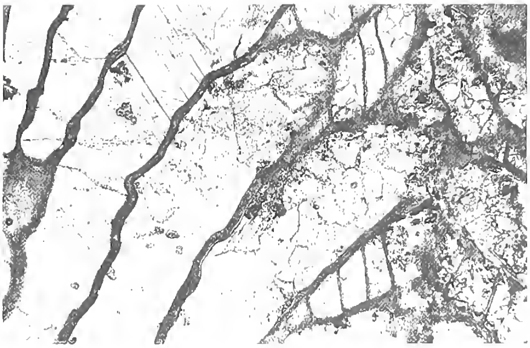
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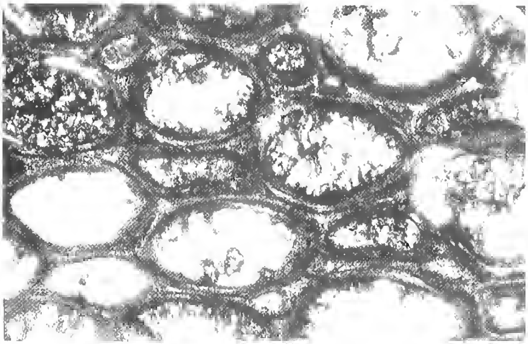
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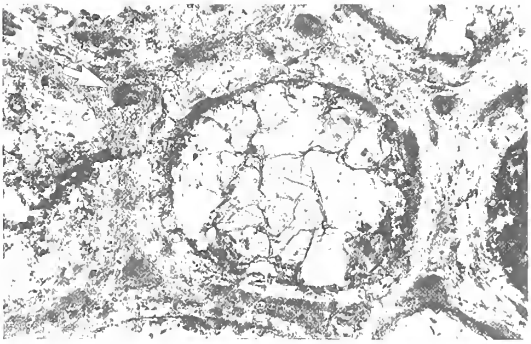
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Paratypes. BMNH PD8183–8194, 8196–8200, 8303–8305; same locality and horizon as holotype.

Etymology. The species is named after Gwyndy Farm, which is adjacent to the type locality.

Diagnosis. Colony ramose. Zooecia, with thick crenulated walls in endozone, parallel branch axis, then curve gradually out to meet zoarial surface. Autozooecia polygonal in transverse section; oval-circular in shallow tangential sections. Mesozooecia oval, originating in outer endozone. Diaphragms rare in autozooecia, present in mesozooecia. Acanthostyles extremely rare; small and inconspicuous in exozone.

Description. Zoaria erect with cylindrical branches, on average 5·2 mm in diameter. The surfaces of all specimens are slightly abraded. Autozooecia generally parallel the branch axis in the endozone and then curve outwards gradually to meet the zoarial surface. The autozooecia within the endozone have thick, highly crenulated walls. The exozone is usually narrow with an average diameter of 1·4 mm. It is recognized by a thickening of the zooecial walls. Autozooecia originate in the endozone where they are polygonal in transverse section, becoming oval-circular in the exozone, as seen in tangential sections of branches. Autozooecial diameters average 0·33 mm by 0·25 mm within the exozone. Diaphragms are usually absent in the autozooecia and, if present, only one or two are found. These basal diaphragms are deflected orally at their junctions with zooecial walls. The diaphragm laminae are all continuous with the autozooecial linings.

Mesozooecia are common and originate in the endozone, their maximum diameter averaging 0·14 mm. They are oval in shape in shallow tangential sections. Orally deflected basal diaphragms are common in the exozone and are spaced on average 0·11 mm apart.

Acanthostyles are rare; when present (e.g. PD8192), they are usually small and very inconspicuous and occur in the outer exozone; their structure is indistinct (Pl. 5, fig. 8).

Autozooecial wall thickness averages 0·08 mm in the exozone. Wall microstructure is composed of steeply inclined, U-shaped laminae and the wall boundaries are dark and granular. The thickness of the endozonal walls enables the microstructure to be clearly seen within them. Some zooecia, especially mesozooecia, are infilled with laminar calcite close to the zoarial surface. In longitudinal section this infilling consists of broad U-shaped laminae.

Conspecific overgrowths have been recognized in a few specimens (e.g. PD8186). They appear continuous with the underlying branch suggesting that they are intrazoarial overgrowths. The overgrowths are composed of exozonal components.

Remarks. *Anaphragma gwyndyense* is distinguished by the thick, highly crenulated nature of the endozonal walls, the numerous diaphragms in the mesozooecia and the small rare acanthostyles. This species is assigned to *Anaphragma* because it fits the redefined genus concept proposed by Boardman (1960). Species of *Anaphragma* possess common laminate acanthostyles whose size can be extremely variable. However, in virtually all specimens of *A. gwyndyense* acanthostyles have not been recognized. This may partly be because the majority of the tangential sections are relatively deep and acanthostyles are only found in the very outer exozone. Alternatively, they may be truly absent.

A. shucknellense was described by Owen (1962) from the Aymestry Limestone (Ludlow Series, upper Silurian), Ludlow District. This species has a few thin diaphragms within the autozooecia; mesozooecia and acanthostyles are absent. This is the only species of *Anaphragma* previously described from the Welsh Basin.

A. gwyndyense is similar to *A. mirabile* Ulrich and Bassler, 1904, known from the upper Ordovician of North America and Estonia, but is primarily distinguished by the presence of mesozooecia, the thick crenulated endozonal walls, and the rare acanthostyles. Three other species of *Anaphragma* have been recognized from the USSR: *A. mirabile* var. *cognata* Bassler, 1911; *A. vetustum* Modzalevskaya, 1953; and *A. minutum* Astrova, 1965. *A. gwyndyense* is readily distinguished from these species by the numerous diaphragms within the mesozooecia. *A. gwyndyense* is very similar to *Hallopora anaphragmoides* Pushkin, 1987 (*in* Ropot and Pushkin, 1987), described from White Russia. Acanthostyles are apparently absent in the Russian species, whereas they have been recognized, albeit rarely, in *A. gwyndyense*.

Order FENESTRATA Elias and Condra, 1957
Suborder PHYLLOPORINA Lavrentjeva, 1979
Family CHASMATOPORIDAE Schulga-Nesterenko, 1955
Genus PINNATOPORELLA gen. nov.

non 1884 *Pinnatopora* Vine; p. 191.
1884 *Pinnatopora* Shrubsole (*in* Shrubsole and Vine); p. 330.
1885 *Pinnatopora* Shrubsole; p. 100.

Type species. Ramipora hochstetteri var. *carinata* Etheridge, 1879: Bala Beds (upper Ordovician Caradoc), Corwen, Gwynedd, Wales.

Diagnosis. Colonies erect and pinnate, branches at same height on opposite sides of the parent branch. Tertiary branches may anastomose. Autozooecia in two longitudinal rows on the frontal side of the colony. Central ridge and striae on colony reverse.

Remarks. Pinnatoporella is similar to the Carboniferous genus *Penniretepora* d'Orbigny, 1849 (redescribed by Olaloye 1974). Both genera have two longitudinal rows of ovoid zooecial apertures on the front of the colony, and a central ridge with striae on the reverse. The difference between them is that the branches of *Pinnatoporella* often anastomose but this never occurs in *Penniretepora* (Olaloye 1974). The Silurian genus *Arcanopora* Shrubsole and Vine, 1882*a* differs from *Pinnatoporella* by the large open apertures (zooecia lack frontal walls) and the presence of three or more rows of autozooecia.

The generic status of *Glauconome* Goldfuss, 1829 (non Gray, 1828), *Penniretopora* d'Orbigny, 1849, *Pinnatopora* Vine, 1884 and *Pinnatopora* Shrubsole (*in* Shrubsole and Vine, 1884) has frequently been discussed (e.g. Ross 1966, p. 121; Olaloye 1974, p. 474; Spjeldnaes 1983, p. 17). A summary of the nomenclatural history is given below with some new evidence regarding the validity of the genus '*Pinnatopora*' and its relationship to *Pinnatoporella*.

Goldfuss (1829) created the genus *Glauconome* and mentioned four species, all Tertiary cheilostomes from the Eiffel. In 1831 he described a fifth species, *G. distincta* from the Silurian of Dudley. Lonsdale (1839) redefined the genus based on additional material from the Wenlock Limestone of Dudley, and not on Goldfuss' original specimens. Lonsdale made *G. distincta* the type species, but this was invalid because the species was not available as the type. The Silurian *G. distincta* has more than two rows of zooecia on each branch, and the zooecia have large open apertures.

The new *Glauconome* is, however, preoccupied by *Glauconome* Gray, 1828 (a bivalve). In an abstract by Shrubsole and Vine (1882*a*, *b*) a new genus *Arcanopora* was proposed with *G. distincta* named as the type species. Vine later (1884) gave the species *Flustra* (?) *parallela* Phillips as the type of *Arcanopora* but this is invalid as the type species has already been validly designated. Bassler (1952) proposed *Glauconomella* as a new name for *Glauconome* Goldfuss, citing *G. distincta* as the type species. As *Glauconomella* Bassler, 1952 and *Arcanopora* Shrubsole and Vine, 1882*a* share the same type species, *Glauconomella* is a junior objective synonym of *Arcanopora*.

In 1849 d'Orbigny proposed the genus *Penniretepora*, with the type species *Retepora pluma* Phillips. This is a Carboniferous species with two rows of 'box-like' zooecia having ovoid apertures. In 1850 d'Orbigny redescribed *Penniretepora*, making *G. distincta* (sensu Lonsdale) the type species and renaming it *P. londsdalei*. This action is invalid and *R. pluma* remains the type species of *Penniretepora*.

Two papers were published in 1884, one by Shrubsole and Vine, the other by Vine, both proposing *Pinnatopora* as a new genus. In Vine's paper of 1884, no type species was given but nine Carboniferous species were mentioned, including *Pinnatopora elegans* Young and Young which was illustrated. *Pinnatopora* has since been placed in synonymy with *Penniretopora* by Bassler (1935). In the 1884 paper by Shrubsole and Vine, no type species was designated but as only *Pinnatopora sedgwicki* was described, this would be regarded as the type species by monotypy; *P. sedgwicki* is an Ordovician species with two rows of autozooecia and ovoid apertures. This species has been

TABLE 1. Summary of the biometric details of all trepostome species from the Slade and Redhill Beds, near Whitland.

Species	ZOW	EXW	MXZD	MNZD	MXMD
Heterotrypa sladei	7·5^{a} (4)^{b} 5·5–10·0^{c}	1·26 (4) 1·14–1·43	0·27 (4) 0·21–0·32	0·23 (4) 0·17–0·3	0·11 (4) 0·06–0·17
Dekayia pengawsensis	11·0 (3) 8·0–13·0	—	0·32 (3) 0·27–0·38	0·29 (3) 0·23–0·36	0·12 (3) 0·04–0·19
Dekayia cf. *crenulata*	7·0 (3) 6·0–8·0	1·1 (2) 1·05–1·14	0·27 (2) 0·23–0·32	0·22 (2) 0·19–0·29	0·12 (2) 0·08–0·15
Leioclema orbicularis	6·38 (8) 5·0–9·0	1·66 (8) 1·33–2·09	0·34 (8) 0·25–0·44	0·25 (8) 0·13–0·36	0·16 (8) 0·1–0·25
Hallopora peculiaris	8·3 (46) 5·0–13·0	1·65 (43) 1·33–2·28	0·37 (41) 0·13–0·57	0·32 (41) 0·19–0·48	0·16 (40) 0·06–0·29
Hallopora cf. *elegantula*	3·17 (3) 2·5–4·0	0·86 (1) 0·86–0·86	0·31 (3) 0·25–0·38	0·26 (3) 0·19–0·34	0·15 (3) 0·1–0·19
Eridotrypa sp.	1·5 (2) 1·5–1·5	0·53 (2) 0·38–0·67	0·15 (2) 0·13–0·19	0·19 (2) 0·1–0·13	0·1 (1) 0·1–0·1
Anaphragma dnestrense	6·43 (35) 4·0–9·0	1·34 (18) 0·95–1·71	0·43 (34) 0·29–0·61	0·33 (34) 0·23–0·42	—
Anaphragma gwyndyense	5·2 (20) 4·0–7·0	1.35 (15) 0·95–1·9	0·33 (13) 0·19–0·49	0·25 (13) 0·17–0·4	0·14 (13) 0·06–0·29

Species	MXED	ZWT	ZMM	DEX	DEN
Heterotrypa sladei	—	0·04 (4) 0·02–0·06	9·36 (4) 7·0–11·0	0·13 (4) 0·06–0·21	0·32 (4) 0·13–0·64
Dekayia pengawsensis	—	0·02 (3) 0·02–0·04	9·14 (3) 7·0–11·0	—	0·48 (3) 0·13–0·86
Dekayia cf. *crenulata*	—	0·03 (2) 0·02–0·04	8·57 (3) 7·0–10·0	0·25 (2) 0·1–0·42	—
Leioclema orbicularis	—	0·12 (8) 0·04–0·19	4·38 (8) 3·5–6·0	0·4 (1) 0·4–0·4	0·23 (3) 0·13–0·38
Hallopora peculiaris	—	0·08 (41) 0·02–0·17	5·24 (40) 3·0–8·0	0·15 (14) 0·02–0·29	0·16 (2) 0·11–0·23
Hallopora cf. *elegantula*	—	0·11 (3) 0·06–0·21	4·9 (3) 4·0–6·0	—	0·17 (3) 0·1–0·23
Eridotrypa sp.	—	0·04 (2) 0·02–0·06	—	0·12 (2) 0·08–0·21	0·21 (2) 0·08–0·34
Anaphragma dnestrense	0·16 (34) 0·04–0·38	0·08 (32) 0·02–0·19	4·6 (34) 3·0–7·0	—	—
Anaphragma gwyndyense	—	0·08 (15) 0·04–0·21	6·22 (14) 4·0–8·0	0·24 (10) 0·11–0·32	0·22 (2) 0·1–0·32

Species	DMEX	DMEN	AD	AZ	AMM
Heterotrypa sladei	0·1 (4) 0·06–0·15	0·18 (2) 0·08–0·27	0·04 (4) 0·03–0·06	1·84 (3) 1·0–3·0	8·8 (3) 5·0–12·0
Dekayia pengawsensis	0·11 (3) 0·06–0·23	—	0·03 (3) 0·02–0·05	—	5·0 (1) 5·0–5·0
Dekayia cf. *crenulata*	0·13 (6) 0·1–0·19	0·15 (3) 0·1–0·17	0·05 (3) 0·03–0·07	1·4 (3) 1·0–2·0	7·2 (2) 6·0–8·0
Leioclema orbicularis	0·08 (8) 0·04–0·19	0·15 (6) 0·08–0·25	0·1 (8) 0·08–0·14	3·8 (8) 2·0–5·0	8·0 (8) 6·0–12·0

Table 1. (*cont.*)

Species	DMEX	DMEN	AD	AZ	AMM
Hallopora peculiaris	0·07 (45) 0·2–0·15	0·13 (43) 0·06–0·23	—	—	—
Hallopora cf. *elegantula*	0·05 (3) 0·02–0·08	0·1 (3) 0·6–0·17	—	—	—
Eridotrypa sp.	0·056 (2) 0·04–0·08	—	—	—	—
Anaphragma dnestrense	—	0·03 (29) 0·01–0·06	10·2 (4) 4·0–18·0	12·0 (4) 4·0–17·0	—
Anaphragma gwyndyense	0·11 (18) 0·04–0·27	—	0·03 (1) 0·3–0·3	—	—

All measurements are in mm except for ZMM, AD and AMM. Abbreviations: a, mean; b, number of specimens; c, range; ZOW, zoarial diameter; EXW, exozonal width; MXZD, maximum autozooecial diameter; MNZD, minimum autozooecial diameter; MXMD, maximum mesozooecial diameter; MXED, maximum exilazooecial diameter; ZWT, autozooecial wall thickness; ZMM, autozooecia mm^{-2}; DEX, distance between exozonal autozooecial diaphragms; DEN, distance between endozonal autozooecial diaphragms; DMEX, distance between exozonal mesozooecial diaphragms; DMEN, distance between endozonal mesozooecial diaphragms; AD, acanthostyle diameter; AZ, number of acanthostyles per autozooecia; AMM, acanthostyles mm^{-2}.

described previously as *Glauconome sedgwicki* Shrubsole (*in* Shrubsole and Vine, 1882). Spjeldnaes (1983) tried to determine which of the two 1884 papers appeared first. He discovered that Shrubsole and Vine's was published in the *Quarterly Journal of the Geological Society of London* on 1 May, 1884 and although he could not find the exact date of issue of Vine's paper in the *Annual Report of the British Association for the Advancement of Science*, he considered it to be late in 1884. He therefore suggested that 'Shrubsole and Vine 1884 was legally issued before Vine 1884 and that *P. carinata* [which Spjeldnaes regarded as a senior synonym of *P. sedgwicki*] therefore is the type species of *Pinnatopora*'.

New evidence has since been found pertaining to the publication date of Vine (1884). The *Register of Serial Publications* at the BMNH records the dates of acquisitions to their General Library. The BAAS Annual Report volume containing Vine's paper was acquired by the BMNH on 30 April 1884, one day before Shrubsole and Vine (1884) was published. Therefore Vine (1884) has priority over Shrubsole and Vine (1884) and the type species of the genus *Pinnatopora* must come from the nine Carboniferous species mentioned by Vine (1884). Among these are *Glauconome elegans* Young and Young which Bassler (1935) named as the genotype. Species of the so-called Ordovician *Pinnatopora*, as exemplified by *P. carinata*, are inappropriately assigned to *Pinnatopora*. They differ from Carboniferous species by the very common anastomosing nature of their branches. The new name *Pinnatoporella* is herein proposed to encompass these species including *Pinnatopora* sensu Shrubsole (*in* Shrubsole and Vine, 1884). One further description of *Pinnatopora* 'gen. nov.' Shrubsole was published in 1885, in the *Proceedings of the Chester Society of Natural Sciences*. This included a description of the species *P. sedgwicki* which would be regarded as the type by monotypy. However, Vine (1884) has priority over this publication.

Distribution. The genus is currently known only from Wales.

Range. Upper Ordovician.

TABLE 2. Summary of the nomenclature and distinguishing characteristics of the pinnate fenestrate genera *Pinnatoporella*, *Arcanopora* and *Penniretepora*

Genus and author	Valid type species	Age of type species	Synonymous genera	Distinguishing characteristics
Pinnatoporella gen. nov.	*Ramipora hochstetteri* var. *carinata* Ethcridge, 1879	Upper Ordovician	*Pinnatopora sensu* Shrubsole and Vine, 1884 *Pinnatopora sensu* Shrubsole, 1885	Anastomosing branches 2 rows of autozooecia Ovoid zooecial apertures
Arcanopora Shrubsole and Vine, 1882	*Glauconome distincta* Goldfuss, 1829	Middle Silurian	*Glauconome* Goldfuss, 1829 *Glauconomella* Bassler, 1935	Non-anastomosing branches 3 or more rows of autozooecia Large open zooecial apertures
Penniretepora d'Orbigny, 1849	*Retepora pluma* Phillips, 1836	Lower Carboniferous	*Pinnatopora* Vine, 1884	Non-anastomosing branches 2 rows of autozooecia Ovoid zooecial apertures

Pinnatoporella carinata (Etheridge, 1879)

Plate 6, figs 1 and 2

1839	*Glauconome distincta* (pars) Lonsdale, p. 49.
1879	*Ramipora hochstetteri* var. *carinata* Etheridge, p. 241, pl. 6.
1882*a*	*Glauconome sedgwicki* Shrubsole (*in* Shrubsole and Vine), p. 245.
1882*b*	*Glauconome sedgwicki* Shrubsole (*in* Shrubsole and Vine), p. 381.
1884	*Pinnatopora sedgwicki* Shrubsole (*in* Shrubsole and Vine), p. 330.
1885	*Pinnatopora sedgwicki* Shrubsole, p. 100.
1908	*Ramipora hochstetteri* Toula var. *carinata* Etheridge; Groom and Lake, p. 572.

Lectotype. Designated herein, NMW 27.110 G37 (Etheridge 1879, pl. 6, fig. 1*a*, *b*); Bala Beds (Caradoc), Garth Gell, Corwen, Gwynedd, Wales.

Paralectotypes. Designated herein, BMNH D48661 (Etheridge 1879, pl. 4, fig. 3), Bala Beds (Caradoc), Corwen, Gwynedd, Wales; and BGS 85495–6 (Etheridge 1879, pl. 4, fig. 2), S. of Cefn Coch, near Llangollen, Gwynedd, Wales.

Additional material. BMNH PD8405 (hand specimen), Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, W. of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. Dolhir Beds (Ashgill), Plas Einion, and Pant, Glyn Ceiriog, Gwynedd, Wales; upper Bala Beds (Caradoc), Corwen, Gwynedd, Wales.

Diagnosis. As for genus.

Description. Zoaria are erect and pinnate, known only from decalcified specimens. The colony from South Wales is 26 mm in height and 32 mm in width. Primary branches are 1 mm in diameter, and secondary branches 0·4 mm in diameter. Secondary branches occur in pairs on opposite sides of the main branch, and are common; tertiary branches also occur. In the lectotype, illustrated by Etheridge (1879, pl. 6, fig. 1*b*), V-shaped fenestrules are observed; they appear to develop by the fusion of adjacent tertiary branches.

The reverse surface of the colony has a central ridge with striae on either side. On the frontal side there are two longitudinal rows of autozooecia. Autozooecial apertures are ovoid in shape, and approximately 0·15 mm in diameter.

Remarks. This species is characterized by the pinnate colony form and two longitudinal rows of ovoid autozooecia. The reverse sides of colonies have a central ridge and are striated.

The species was first described by Etheridge (1879) as a variety of the species *Ramipora hochstetteri* from the Permo-Carboniferous of Spitzbergen. *Ramipora hochstetteri* is, however, a cystoporate (Utgaard *in* Boardman *et al*. 1983; Nakrem 1988). Shrubsole (*in* Shrubsole and Vine 1882) described a new species *Glauconome sedgwicki* and two years later (*in* Shrubsole and Vine 1884) re-assigned it to a new genus, *Pinnatopora*. The synonymy list for this species includes the variety described by Etheridge. *Pinnatopora* Shrubsole *in* Shrubsole and Vine, 1884 is preoccupied by *Pinnatopora* Vine, 1884 (discussed above p. 95) and the name *Pinnatoporella* is here erected. The variety name proposed by Etheridge (1879) is raised to specific level and *sedgwicki* becomes a junior synonym. *P. carinata* is the only known species of *Pinnatoporella*.

Order CYSTOPORATA Astrova, 1964
Suborder FISTULIPORINA Astrova, 1964
Family FISTULIPORIDAE Ulrich, 1882
Genus FISTULIPORA M'Coy, 1849

Fistulipora sp.

Plate 6, figs 3 and 4

Material. BMNH PD8236*c*, 8385*f*, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Description. Zoaria are only recognized in randomly oriented peels and appear as long bands, on average 1 mm in height.

Autozooecia are perpendicular to the base. Vesicles are oval in longitudinal section, with irregular bases where they interlock. The average distance between zooecia is 0·53 mm. Zooecial walls are thin throughout the colony and usually straight, although adjacent vesicular tissue can indent them, giving an undulating appearance. Vesicular tissue is abundant between autozooecia throughout the colony. There is periodically a marked thickening of the vesicle roofs from 0·09 mm to 0·15 mm.

Lunaria are present and seen in longitudinal section as hyaline rods on the sides of the autozooecia.

The microstructure is hard to distinguish but laminar walls can be identified.

Remarks. No species of *Fistulipora* have previously been described from the Ordovician of the Welsh Basin. Owen (1962, 1969) described several Silurian members of the genus from Shropshire. *F. strawi* Owen, 1962 has similar thin walls and abundant vesicular material to the Ordovician specimens but lacks basal diaphragms and has less distinct lunaria. The species *F. nummulina* Nicholson and Foord, 1885, described by Owen (1969) from Dudley, has similar distinct lunaria to the Pengawse Hill material but less abundant vesicles and no basal diaphragms. The Pengawse Hill species is left in open nomenclature until more complete specimens can be examined.

Suborder CERAMOPORINA Bassler, 1913
Family CERAMOPORIDAE Ulrich, 1882
Genus CERAMOPORELLA Ulrich, 1882

Ceramoporella distincta Ulrich, 1890

Plate 6, figs 5–8

1890	*Ceramoporella distincta* Ulrich, p. 464, pl. 39, figs 6, 6*a*.
1908	*Ceramoporella distincta* Ulrich; Cummings, p. 799, pl. 10, fig. 7; pl. 11, figs 2, 2*a*.
1909	*Ceramoporella distincta* Ulrich; Grabau and Shimer, p. 122.
1953	*Ceramoporella distincta* Ulrich; Bassler, p. G81, text-figs 44, 2*a*, *b*.
1968	*Ceramoporella distincta* Ulrich; Utgaard, p. 1405, pl. 181, fig. 4; pl. 182, figs 1–3.
1973	*Ceramoporella distincta* Ulrich; Utgaard, figs 16, 23.
1984	*Ceramoporella distincta* Ulrich; Karklins, p. 189, pl. 38, figs 1, 4.

Material. PD8386–8388, 8395, Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed, Wales (SN 164170).

Other occurrences. Eden and Waynesfield Formation, Cincinnati; Brannon and Millersburg Members, Shermanian Stage, Lexington Limestone, Kentucky.

Description. Zoaria encrusting, consisting of up to five superimposed layers of zooecia. The basal layer, observed in thin section, has an average thickness of 0·8 mm, and the basal laminae of the zooecial layers have a laminated microstructure. It is difficult to distinguish endozone from exozone. In the endozone the autozooecia are slightly recumbent and the zooecial walls are thin and straight. In the exozone the walls remain straight and the zooecial apertures in shallow tangential section are circular-polygonal and on average 0·26 mm in diameter. Lunaria are abundant throughout the colony.

Diaphragms are occasionally present in the autozooecia, sometimes pierced by pores, and apparently aborally deflected and continuous with the zooecial linings. These diaphragms frequently occur at the same level in adjacent zooecia. Basal diaphragms are rare.

Small exilazooecia are present in the outer endozone and exozone. These contain no diaphragms and are rounded in shallow tangential section, on average 0·09 mm in diameter.

Communication pores have not been observed. Possible acanthostyle-like structures have been observed but not identified conclusively. The microstructure is hard to distinguish but appears to be laminar.

Remarks. The species is characterized by the multilayered zoaria, thin autozooecial walls, sparse diaphragms and the presence of distinct lunaria. It is very similar to *Ceramoporella distincta* Ulrich, 1890, recently re-described by Karklins (1984, p. 189), from the McMiken Member, Eden Formation (upper Ordovician), Cincinnati, Ohio, USA. The main difference is that the specimens from Wales have fewer exilazooecia than those from North America.

EXPLANATION OF PLATE 6

Figs 1–2. *Pinnatoporella carinata* (Etheridge, 1879). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD8405, mould of a pinnate colony, ×5. 2, BMNH PD8405, mould of a pinnate colony showing rounded autozooecial apertures, ×9.

Figs 3–4. *Fistulipora* sp. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 3, BMNH PD8385*f*, longitudinal section, ×48. 4, BMNH PD8385*f*, longitudinal section, showing the vesicular tissue between the autozooecia and lunaria at the side of the autozooecia, ×68.

Figs 5–8. *Ceramoporella* aff. *distincta* Ulrich, 1890. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 5, BMNH PD8386, longitudinal section, ×28. 6, BMNH PD8386, longitudinal section showing specimen encrusting a halloporid colony, ×18. 7, BMNH PD8386, longitudinal section, showing subterminal diaphragms at the same level in adjacent autozooecia, ×38. BMNH PD8387, tangential section, showing lunaria, ×110.

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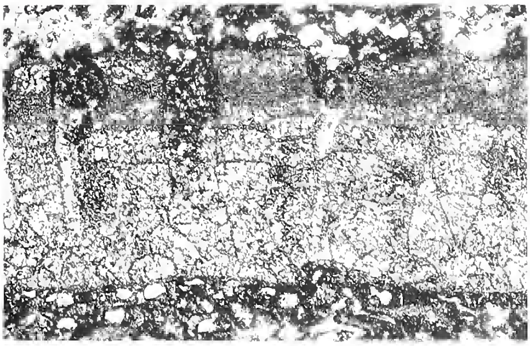

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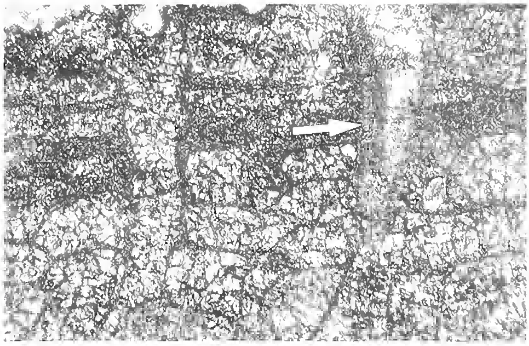

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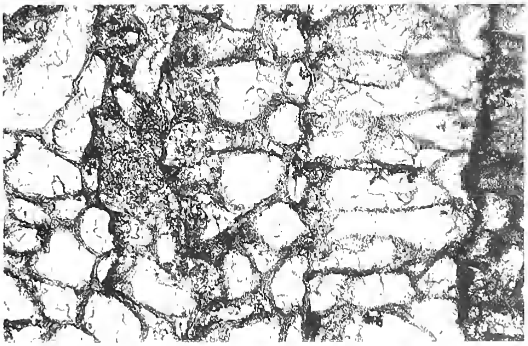

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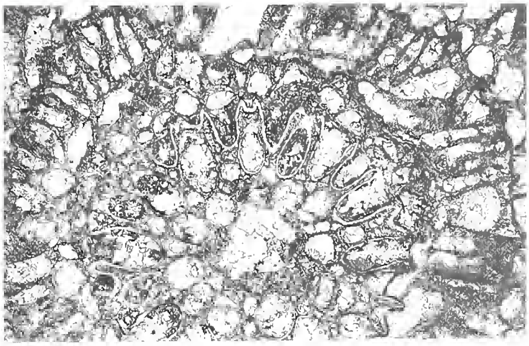

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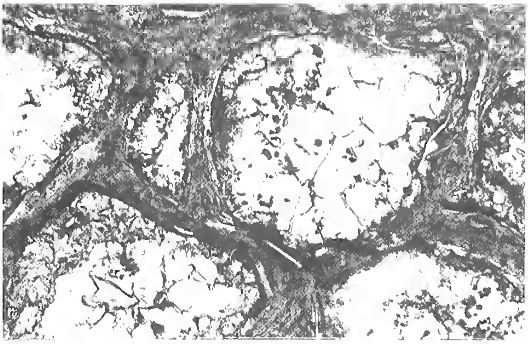

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BUTTLER, *Pinnatoporella*, *Fistulipora*, *Ceramoporella*

Family RHINOPORIDAE Miller, 1889

Emended diagnosis. Zoaria thin, encrusting or bifoliate. Autozooecial apertures elongate. Hyaline lunaria present. Walls laminated or granular-prismatic. Autozooecia recumbent close to the basal lamina, bending to become perpendicular to base in later ontogeny. Small polygonal exilazooecia present between autozooecia. Communication pores often present, up to three per zooecium. Anastomosing tunnel structures present, with roofs elevated above zoarial surface, some tunnels containing barriers.

Remarks. The family Rhinoporidae is characterized by the unusual tunnel structures found in the two constituent genera *Rhinopora* and *Lichenalia*. It was previously placed within the suborder Fistuliporina because of the occasional presence of blister-like vesicular tissue. This tissue has been described as irregular, and unlike that commonly found in fistuliporines. Vesicular tissue has been observed in *Lichenalia* (Utgaard *in* Boardman *et al.* 1983, fig. 192, 2*b*) but does not appear to be a consistent feature in all colonies. The tunnel structures are easy to mistake for vesicles in section when they have been overgrown by the colony. Well-preserved specimens of *Rhinopora* and *Lichenalia* have been examined during this study and abundant communication pores observed. These are common in the suborder Ceramoporina but have not been identified conclusively in Fistuliporina. Therefore, the family is herein reassigned to Ceramoporina.

Genus LICHENALIA Hall *in* Silliman, Silliman and Dana, 1851

Type species. Lichenalia concentrica Hall, 1852; Rochester Shale (middle Silurian), Lockport, New York State, USA; by monotypy.

Emended diagnosis. Zoaria encrusting with laminated basal layer; autozooecia with long recumbent portion, walls thin and laminated. Diaphragms uncommon. Small polygonal exilazooecia present between autozooecia. Lunaria hyaline, elevated at colony surface. Bifurcating and anastomosing tunnel structures are common, some with internal partitions. Communication pores may be present in exozone.

Remarks. The diagnosis has been revised from Utgaard (*in* Boardman *et al.* 1983, p. 407) to include the presence of communication pores.

Distribution. The genus was previously known from North America and the USSR.

Range. Upper Ordovician–middle Silurian.

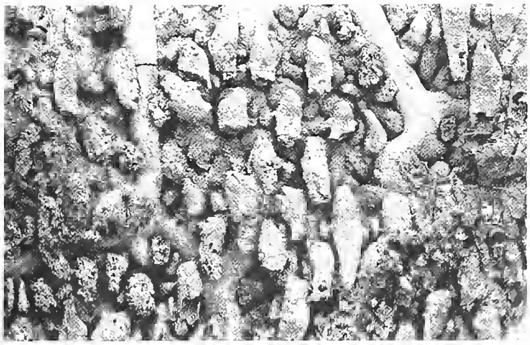
EXPLANATION OF PLATE 7

Figs 1–2. *Lichenalia* cf. *concentrica* Hall, 1852. Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 1, BMNH PD9873, decalcified colony showing unusual tunnel structures meandering between the autozooecia, ×15. 2, BMNH PD9873, tunnel structures, ×34.

Figs 3–6. *Lichenalia* cf. *concentrica* Hall, 1852. Wenlock Shales (Homerian, Wenlock, Silurian), Dudley, West Midlands. 3, BMNH PD9885, surface of colony showing abundant communication pores and small polygonal mesozooecia, ×31. 4, BMNH PD9885, bifurcating tunnel structure, ×15. 5, BMNH PD9885, tunnel overgrown by a subsequent layer of the colony, ×40. 6, BMNH PD1886, tangential section showing bifurcating tunnel structures, ×28.

Figs 7–8. *Kukersella borealis* (Bassler, 1911). Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, west of Whitland, Dyfed. 7, BMNH PD8154*a*, *b*, longitudinal and transverse sections, ×18. 8, BMNH PD8236*a*, transverse section with abundant pseudopores in frontal wall, ×43.

PLATE 7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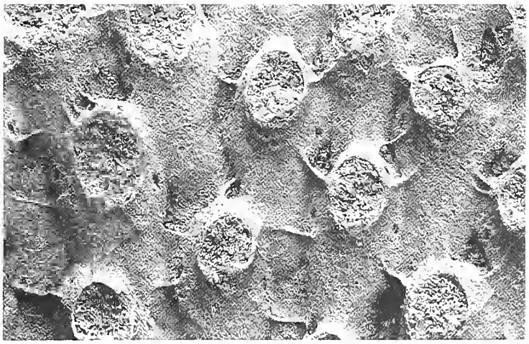
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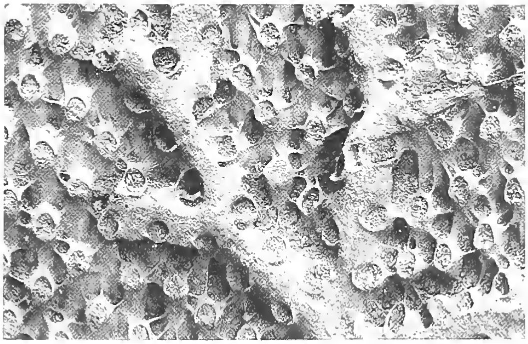
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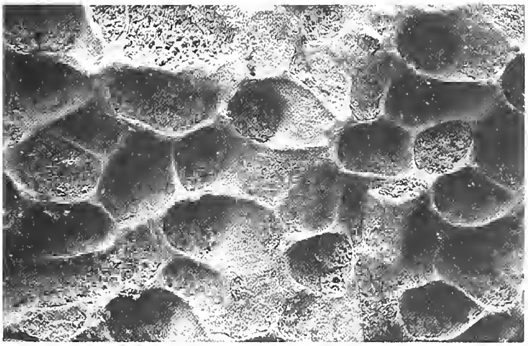
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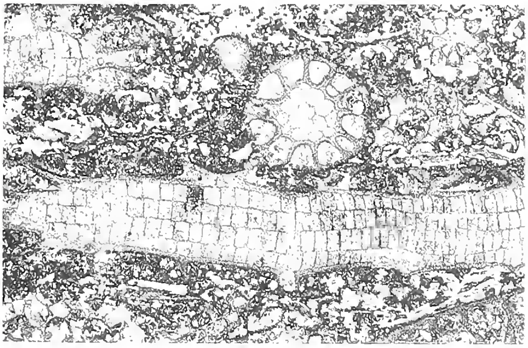
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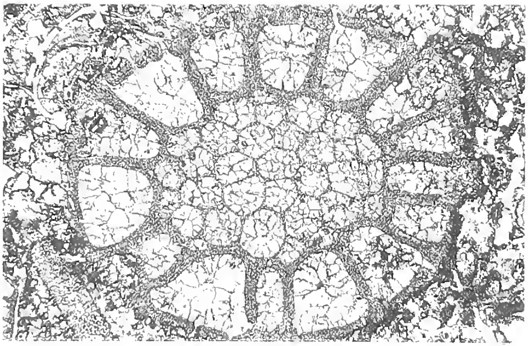
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BUTTLER, *Lichenalia*, *Kukersella*

Lichenalia cf. *concentrica* Hall, 1852

Plate 7, figs 1–6

Material. BMNH PD9885–6 (hand specimens); Wenlock Shale, Dudley, West Midlands. BMNH PD9871, 9873, 9874, 9876, 9878 (hand specimens); Slade and Redhill Beds (upper Rawtheyan, Ashgill), A40 Pengawse Hill diversion, W. of Whitland, Dyfed, Wales (SN 164170).

Description. All colonies are unilaminate and encrusting. The Silurian specimens encrust brachiopods, whereas the Ordovician material forms unilaminar hollow cylindrical colonies which may have encrusted a soft-bodied organism such as a hydroid.

Autozooecia have a recumbent portion in contact with the basal lamina and then bend to become perpendicular to the base. Autozooecial apertures are rounded with an average diameter of 0·22 mm by 0·16 mm. Small polygonal exilazooecia occur between the autozooecia (average maximum diameter is 0·08 mm). Hyaline lunaria are observed in the autozooecia in shallow tangential section. Rare basal diaphragms have been recognized.

Bifurcating and anastomosing tunnel structures are common, positioned a distance from the edge of the colony (2 mm in PD9885). The tunnels are on average 0·21 mm wide and extend for 1·11 mm in length between bifurcations. At the site of bifurcation a crescent-shaped exilazooecium occurs. The tunnels are divided internally by thin-walled barriers.

Communication pores are present in the exozone, commonly two, but up to three, pores per autozooecium. They are situated on either side of the autozooecial aperture, occasionally with one in between.

Microstructure is hard to distinguish but appears to be laminar.

Remarks. The species *Lichenalia concentrica* Hall has been recognized in North America from the Rochester Shale (middle Silurian), New York State and Ontario (Hall 1852; Bassler 1906; Hewitt and Cuffey 1985), and in the USSR from the Borkholm Limestone, Borkholm, Estonia (Bassler 1911). *Lichenalia* cf. *concentrica*, described in the present study, is very similar to previous descriptions of *L. concentrica*, e.g. by Bassler (1906) and Hewitt and Cuffey (1985). The major difference is the presence of communication pores, which have not been recognized previously. This difference may be significant or merely due to the exceptional preservation of the material described herein from Dudley. The majority of examples of *Lichenalia* described previously do not show the frontal surface of the colony as it adheres to the rock matrix, and communication pores may therefore have been present but not observed. The type material from the Rochester Shale (middle Silurian), Lockport, New York State, USA, needs to be re-examined in conjunction with this new British material to establish if they are indeed conspecific.

Order CYCLOSTOMATA Busk, 1852
Family CROWNOPORIDAE Ross, 1967
Genus KUKERSELLA Toots, 1952

Kukersella borealis (Bassler, 1911)

Plate 7, figs 7 and 8

Description. Colony erect with narrow subcylindrical branches (average diameter 1·08 mm), arising from an encrusting base. Endozonal zooecia are very thin-walled and are oriented parallel to the branch growth direction to form an axial bundle which reaches the colony surface only at the distal growth tips. Abundant, closely-spaced (0·09 mm) diaphragms occur throughout the length of the endozonal zooecia and are deflected orally at their junction with vertical interzooecial walls.

Exozonal zooecia surround the axial bundle of endozonal zooecia. They are thick-walled, average 0·48 mm in length and their walls contain sparse communication pores at levels close to the colony surface. Occasional diaphragms are developed at levels close to the colony surface. They are deflected orally where they meet the interzooecial walls. Frontal walls of exozonal zooecia have distal subcircular apertures with an average diameter of 0·15 mm and slight peristomes. Frontal walls are densely pseudoporous, the pseudopores being variable in size but consistently large, on average 0·02 mm in diameter. They are crater-like in external morphology, with funnel-shaped openings.

The encrusting bases are composed entirely of zooecia resembling those of the exozone in erect branches.

Remarks. A more complete description of this species and a synonymy may be found in Buttler (1989).

BIOGEOGRAPHICAL COMPARISONS

A total of twelve genera have been recognized from the Slade and Redhill Beds at Pengawse Hill. One, *Pinnatoporella*, has been described only from Wales, whilst the rest are cosmopolitan. A wide generic distribution may have been caused by a long-lived, planktotrophic larval phase which encouraged dispersal. This was suggested for the Ordovician genus *Orbipora* by Taylor and Cope (1987). Living cyclostomes have non-planktotrophic larvae but Taylor and Cope consider that some early stenolaemates may have inherited a planktotrophic larval stage from their inferred ctenostome ancestors.

Of the fifteen species identified from this locality seven have not been previously recognized elsewhere. Three of these are new species and the rest are left in open nomenclature. It is difficult to know whether this is true endemism or the result of sampling and/or preservation. Three species have very wide geographical ranges: *Kukersella borealis*, *Hallopora elegantula* and *Lichenalia concentrica*. They have all been described previously from both North America and Baltoscandia.

The Welsh taxa show the greatest affinity with Baltoscandia, sharing six of the fifteen species. The faunal similarities between Baltoscandia and the Anglo-Welsh Region have been examined in detail for other groups (e.g. Cocks and Fortey 1982; Vannier *et al.* 1989), although poor knowledge of British bryozoans has previously prohibited comparison. The bryozoans support the hypothesis that Tornquist's Sea, which separated the two regions during the early Ordovician, was no longer a physical structure effecting faunal separation in the late Ordovician. The exact time of its closing is hard to ascertain but the similarity in faunas from the Caradoc onwards suggests that by the late Ordovician Tornquist's Sea was nearly if not actually closed.

North America, or Laurentia, was separated during the lower Ordovician from Baltoscandia and the majority of the British Isles by Iapetus. Faunal and structural studies have examined the exact timing of the closure. Pickering *et al.* (1988), using a variety of palaeontological, stratigraphical, structural, geophysical and igneous evidence, considered that by the end of the Ordovician Iapetus was partially closed with only marine seaways persisting to the mid-Silurian. During the late Ordovician Iapetus did not form an impenetrable barrier to the bryozoans. Four species (17% of the fauna) from Pengawse Hill are also known from the early Palaeozoic of North America.

Only one species (*Dekayia* cf. *crenulata*) from Wales is similar to the bryozoan fauna described from the Montagne Noire region of France. This region would have formed part of Gondwana, which was separated from Laurentia, the British Isles and Baltoscandia during the late Ordovician by the Rheic Ocean, explaining why the similarity of the two faunas is minimal.

Any biogeographical findings concerning bryozoans can only be preliminary because of the poor knowledge of British (and European) Ordovician bryozoans, especially when compared with other groups. This emphasizes the great need for further research and the importance of systematic studies of British Ordovician bryozoans.

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MIDDLE ORDOVICIAN BIVALVES FROM SPAIN AND THEIR PHYLETIC AND PALAEOGEOGRAPHIC SIGNIFICANCE

by CLAUDE BABIN *and* JUAN-CARLOS GUTIÉRREZ-MARCO

ABSTRACT. The rich bivalve fauna from the Middle Ordovician of Spain is reviewed, and some new taxa established: *Dulcineaia manchegana* gen. and sp. nov., *Praenucula sharpei* sp. nov. and *Ekaterodonta hesperica* sp. nov. Some palaeotaxodontids probably had archaic characters, such as the dentition of *Ekaterodonta* and the pedal muscles of *Myoplusia*. The common trend towards the production of crenulated teeth among actinodonts and their descendants is underlined; *Dulcineaia* is a new example among Redoniidae. The comparison with the crenulations of some paleotaxodontids does not show any general constraints governing the evolution of microcrenulations. Bivalve distribution within the *Selenopeltis* province is apparently complex with some endemics during the Middle Ordovician. The Spanish faunas were largely dominated by small endobenthic shells which suggests a cool-water area.

THE Middle Ordovician bivalve molluscs from the shales of the Hesperian Massif were described by Sharpe (1853) from Portugal and by de Verneuil and Barrande (1856) from Spain. Since then, these faunas have not been revised. In contrast, other groups, trilobites, graptolites, echinoderms, have provided the basis of numerous studies which have enabled a precise biostratigraphy for the Llanvirn and Llandeilo series to be established in the Hesperian Massif (Hamman 1974, 1983; Hamman *et al.* 1982; Romano 1982; Gutiérrez-Marco *et al.* 1984*b*; Rábano 1984, 1988; Gutiérrez-Marco 1986). The only indications of bivalves are a list of species by Gutiérrez-Marco *et al.* (1984*b*), a figure of *Redonia* cf. *deshayesi* from the Ossa Morena Zone (Gutiérrez-Marco *et al.*, 1984*a*) and the description of a new cycloconchid (Babin and Gutiérrez-Marco 1985). Similar faunas have been the subject of detailed researches in the Armorican Massif (Babin 1966, 1977; Bradshaw 1970). Increasing interest has been given to other Lower and Middle Ordovician bivalve faunas elsewhere (Pojeta 1971; Morris and Fortey 1976; Pojeta and Gilbert-Tomlinson 1977; Pojeta 1978; Morris 1978, 1980; Babin 1981, 1982; Babin *et al.* 1982). Thus, it is appropriate to revise the systematics of these numerous and diverse molluscs in a modern framework, and to discuss their phyletic and palaeogeographical significance.

This paper is a contribution to Project ID-456 ('Biostratigraphy and palaeoecology of the Lower Paleozoic rocks of SW Hesperian Massif') of Comisión Acesora de Investigación Científica y Técnica Consejo Superior de Investigaciones Científicas, 1985–1988 programming.

GEOLOGICAL SETTING OF SPANISH MIDDLE ORDOVICIAN BIVALVES

We have studied 2400 bivalve samples from 87 localities widely distributed along the Spanish part of the Hesperian Massif. This massif comprises a large area of the Iberian Peninsula and contains the most extensive outcrops of Ordovician rocks known in the European Hercynian fold belt. Text-figure 1 shows the approximate position of the fossil localities. Their detailed locations have been deposited with the British Library, Boston Spa, Yorkshire, UK, as Supplementary Publication No. SUP 14041 [6 pages].

The bivalve faunas come from several formations, composed mainly of shales with scarce sandstones, the latter predominating only in the youngest beds of the succession. They can all be assigned to the 'Tristani Beds' of early authors, which have been divided into a number of

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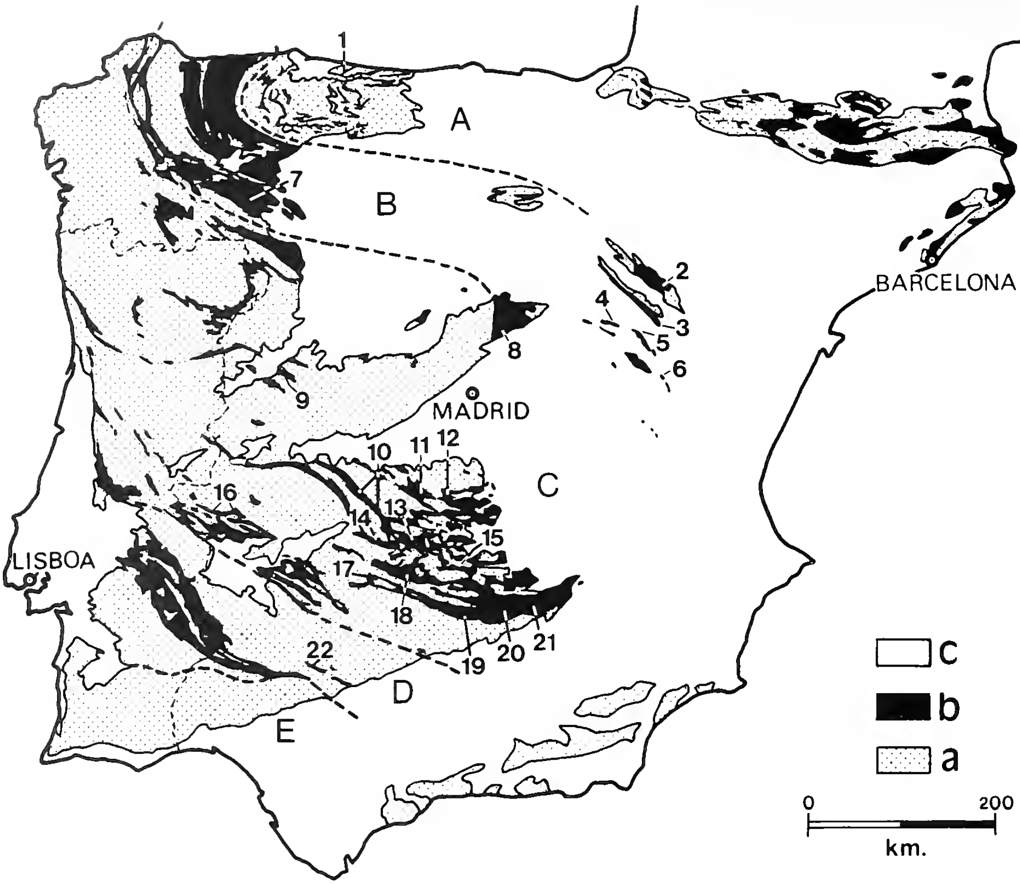
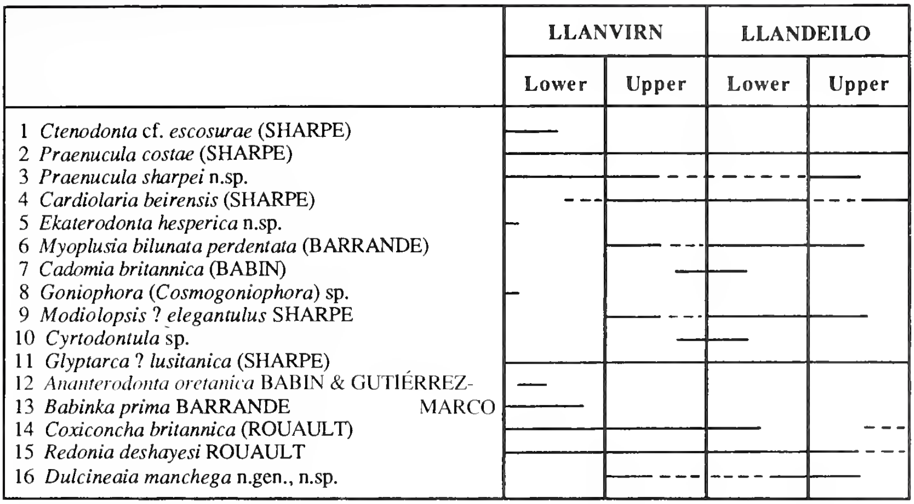


TEXT-FIG. 1. Map showing outcrops of Ordovician rocks in the Iberian Peninsula in solid black with the studied Lower Ordovician bivalve localities. Symbols: a, Precambrian and Palaeozoic rocks; b, Ordovician outcrops; c, post-Palaeozoic cover. A–E, structural zones of the Hesperian Massif: A, Cantabrian zone; B, West-Asturian-Leonese zone (and its southern extension in the Iberian Cordillera); C, Central-Iberian zone; D, Ossa-Morena zone; E, South-Portuguese zone. Fossil localities: 1, 'Sueve'; 2, Fombuena-Herrera (FB, LU, HERR); 3, Calamocha (PO); 4, Aragoncillo (CR, PS); 5, El Pobo (PD); 6, Geo de Albarracin (GA); 7, Truchas (TR); 8, El Atazar (AT); 9, La Bastida (LB); 10, Alia-Navalpino (PSV, HM, RA); 11, Navas de Estena-Retuerta (NE, RE); 12, Ventas (VPA); 13, Benazaire-Puebla de Don Rodrigo (Hd, PR, PI); 14, Herrera del Duque (HD); 15, Pozuelos-Corral de Calatrava (PZ, CO); 16, Sierra de San Pedro (SVA, PC); 17, Santa Eufemia (SEU); 18, Almadén (AC, AM, CHI, GS); 19, Fuencaliente (FU); 20, Calzada-Viso del Marquès (CC, VM); 21, Sierra Morena oriental (ALAM); 22, Cazalla de la Sierra (CS).

formations as summarized and correlated by Hammann *et al.* (1982) and Gutiérrez-Marco *et al.* (1984*a*, in press).

Most of the bivalves are preserved as internal/external moulds in shales, silty nodules and the sandstones; rare casts of specimens with conjoined valves replaced by hematitic or silty materials have seldom been found.

Text-figure 2 shows the stratigraphic distribution of the species based on accompanying fossils of biostratigraphical value (graptolites, trilobites, brachiopods and microfossils). Nevertheless, it has been shown elsewhere that there is difficulty in correlating the Spanish Ordovician with the British



TEXT-FIG. 2. Stratigraphic distribution of Spanish Middle Ordovician bivalve species.

stratotypes of the Llandeilo Series. For this reason, some authors adopt the Bohemian Dobrotivá Series (Havlíček and Marek 1973), with which the Ordovician sequences of the Southern Gondwanan platform ('Mediterranean area') are also easier to correlate. The Dobrotivá Epoch is, however, a possible equivalent of the global standard Teretiusculus Zone. Thus, with reservation, we use the Llandeilo Series in spite of controversy (Whittington *et al.* 1984).

SYSTEMATIC PALAEONTOLOGY

The classification used by Pojeta (1987) is adopted here. The morphological indexes used in some descriptions are those defined by Babin (1966, p. 28). If not otherwise cited, figured and described specimens are in the Department of Palaeontology, Complutense University of Madrid, Spain. Complementary material is housed in the Laboratory of Palaeontology, University of Brest (LPB), in the Université Claude Bernard – Lyon I (FSL), in the British Museum of Natural History, London (BMNH) and in the Národní Museum of Prague.

Class BIVALVIA Linnaeus, 1758
Subclass PALAEOTAXODONTA Korobkov, 1954
Order NUCULOIDEA Dall, 1889
Superfamily CTENODONTACEA Wöhrmann, 1893
Family CTENODONTIDAE Wöhrmann, 1893
Genus CTENODONTA Salter, 1852

Type species. *Tellinomya nasuta* Hall, 1847, by subsequent designation of Salter (1859, p. 34).

Diagnosis. Nuculaniform ctenodontids lacking prominent concentric ornament.

cf. *Ctenodonta escosurae* (Sharpe, 1853)

Plate 1, figs 1–4

cf. 1853 *Leda escosurae* Sharpe, p. 151, pl. 9, fig. 8.

Material. Two internal moulds (one right valve and one left valve), CR II 2161/OR.

Locality and stratigraphical range. Basal shales of La Venta Formation, Aragoncillo Massif (Iberian Cordillera, Castilian Branch); lowermost Llanvirn.

Description and discussion. Small shell (respectively 13 and 10·5 mm long) with a weak beak situated at the anterior third. Anterior margin and ventral side convex; maximum height located exactly behind the umbo. Posterior end gently elongate and rounded; a very faint depression on the posterior part of the shell produces a discrete inflexion of the ventral margin between the posterior fourth and fifth parts. Characters of the hinge plate unknown. Anterior adductor muscle scar posteriorly fringed by a small high and broad septum. Posterior adductor scar poorly visible and anteriorly limited by a weak undulation of the valve.

Sharpe's material of *Leda escosurae* is BMNH Pl. 4106 (internal mould of a bivalve specimen, figured by Sharpe, pl. 9, fig. 8, which must be considered as lectotype; figured here, Pl. 1, figs 1 and 2) and BMNH Pl. 4138 (internal mould of a right valve, paralectotype).

Sharpe's types are nuculaniform with their elongate posterior end, but the dentition, with numerous chevron-shaped teeth, has no resilifer. Thus these forms must be referred to *Ctenodonta* as used since McAlester (1968) and Pojeta (1971) for Nuculoida without a resilifer and with a rostrate end. Our specimens have an outline similar enough to that of *Ctenodonta escosurae*, but their dentition is not preserved and we must leave them in open nomenclature. Barrande (1881, pls 269 and 270) figured several 'species' of '*Leda*' from the Ordovician of Bohemia, but they belong to other genera and are different from *C. escosurae* (Pfab 1934). There are many elongate shells in the Ordovician, and they probably belong to different families or even different orders (e.g. *Thoralia* Morris, 1980 = *Miquelana* Babin, 1982, junior synonym from the Arenig of the Montagne Noire); unfortunately, the material is often poorly preserved.

Superfamily NUCULACEA Gray, 1824
Family PRAENUCULIDAE Pfab, 1934

Remarks. Since the revision by McAlester (1968) of the type material, efforts have been made to homogenize the generic designations of palaeotaxodontids from the Lower Palaeozoic. However, some confusion persists because these small bivalves are numerous, variable, sometimes polymorphous and are often badly preserved or distorted. Among the praenuculids, Tunnicliff (1982) has discussed the difficult distinctions between *Praenucula*, *Praeleda*, and *Deceptrix*. We shall try to apply this author's criteria to distinguish *Praenucula* (anterior and posterior teeth subsimilar in size and number; umbo lying in the posterior half) and *Deceptrix* (= *Praeleda*) (posterior teeth smaller and more numerous than the anterior; umbo lying in the anterior half; adductor muscle scars larger and more ventral than in *Praenucula*.)

Genus PRAENUCULA Pfab, 1934

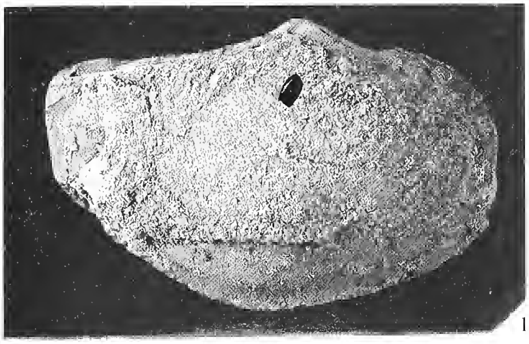
Type species. *Praenucula dispar expansa* Pfab, 1934 (from the Sarka Formation, Llanvirn of Bohemia) by original designation of Pfab, 1934 (pp. 234–235). See discussion under Praenuculidae above.

EXPLANATION OF PLATE 1

Figs 1 and 2. *Ctenodonta escosurae* (Sharpe, 1853). Lectotype (BMNH, Pl. 4106), Middle Ordovician, Portela de Loredo, Serra de Bussaco (Portugal). 1, right view, 2, cardinal view. Both ×4.

Figs 3 and 4, cf. *Ctenodonta escosurae*. Aragoncillo Massif (Iberian Cordillera), basal part of La Venta Formation, lowermost Llanvirn. 3, internal mould of a right valve (CR-II 2 161/OR), ×4. 4, internal mould of a left valve (CR-II 2 161/OR), ×4.

Figs 5–9. *Praenucula costae* (Sharpe, 1853). 5–8, Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo; 5, internal mould of a right valve showing numerous borings on the ventral part (CC-I 2 169/OR), ×4; 6, detail of the postero-umbonal part of an internal mould of a right valve, the muscle scars (posterior adductor and pedal accessory) show growth lines; some borings are present (CC-I 2 166/OR), ×8; 7, internal mould of a left valve (CC-I 2 168^{bis}/OR), ×4. 8, latex replica of the same, ×4. 9, Ventas con Peñas Aguilera (Toledo), lower part of the Navas de Estena Shales, Lower Llanvirn; internal mould of the continuous dentition of the right valve of a young specimen (VPA 2 171/OR), ×8.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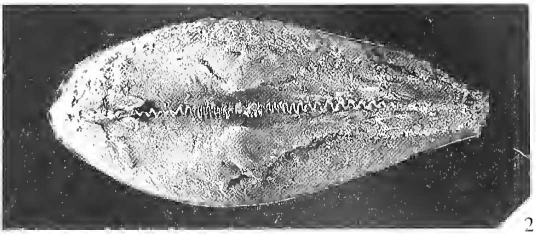
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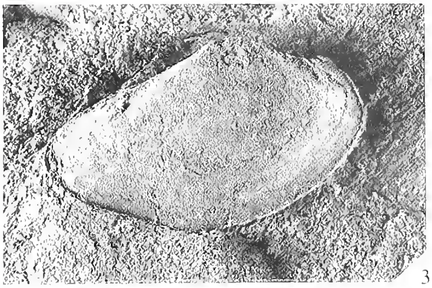
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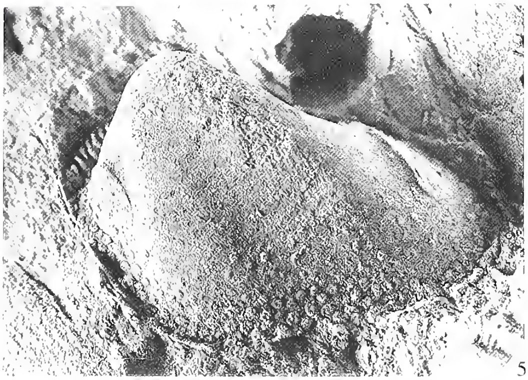
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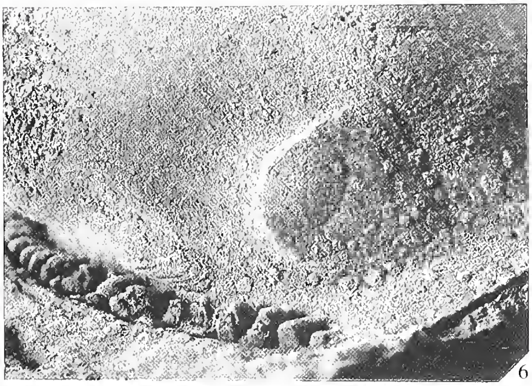
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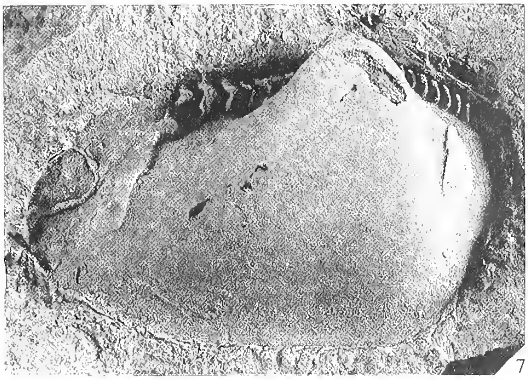
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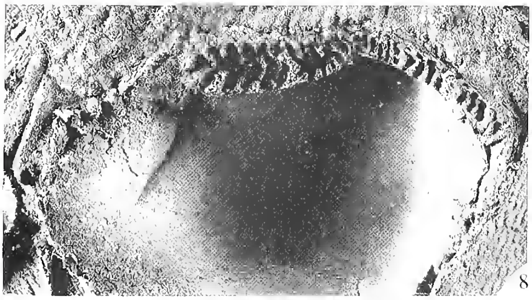
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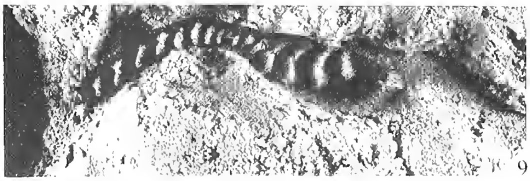
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BABIN and GUTIÉRREZ-MARCO, Middle Ordovician Bivalvia

Praenucula costae (Sharpe, 1853)

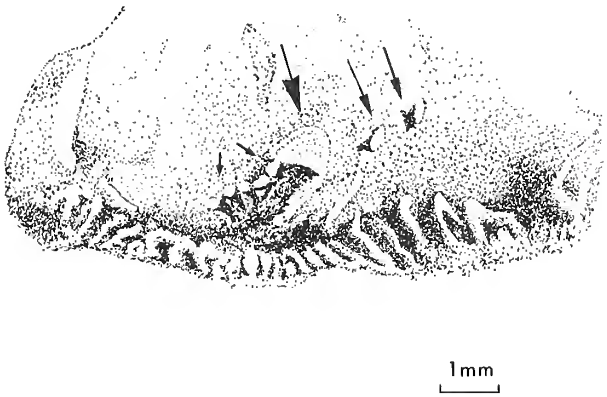
Plate 1, figs 5–9

1853 *Nucula costae* Sharpe, p. 149, pl. 9, fig. 4.
1970 *Praeleda costae* (Sharpe), Bradshaw, p. 630, text-figs 7–10 (synonymy).

Material. About 320 internal moulds.

Localities and stratigraphical range. Lower Llanvirn to Upper Llandeilo (muddy and sandy facies) of the Cantabrian zone (Sueve), West Asturian-leonese zone (TR-III), Iberian Cordillera (FB-IV, GA-II, HERR-I, PD-I, PO-I), and 34 localities in the Central-Iberian zone (AC-II, ALAM-III, Albadalejo, CC-I & II, CHI-IV, CO-XII and XIV-XVI, HD-IV-VI, HM-II and IV, La Carcel, La Vibora, NE-IV & VII, PI-IV, PR-IX, PSV-III-V, PZ-III, RA-I, IA, II, IVB and VI, SEU-II, SP-IV, VM-I, VPA). This species is particularly common in RA-I, CC-I, VPA, PSV-III/IV and La Vibora.

Description. Shell small, convex, with a strong umbo lying in the posterior half and prominent convex cardinal margin. Ventral margin also convex, the posterior side more or less rounded and the anterior side truncate. In juvenile forms the adductor scars are poorly impressed, but in adults they are more marked. Anterior adductor scar large, oval, parallel with the anterior margin and strongly impressed on its posterior side. Posterior scar smaller and round. Two pedal accessory scars always present; one adjacent to the anterior adductor scar on its dorsal side; the other is elongate and situated half-way along the posterior hinge plate. One specimen (CC 2166/OC) shows growth lines on this scar and on the posterior adductor scar (Pl. 1, fig. 6). Specimen RA-I 2167/OR has other scars near the extremity of the umbo (Text-fig. 3).



TEXT-FIG. 3. *Praenucula costae* (Sharpe, 1853). Umbonal view of an internal mould of a left valve (RA-I 2 167/OR) showing accessory muscle scars: two small anterior scars (medium arrows), one umbonal scar (large arrow) and four very small posterior scars (between the fine arrows).

The dentition comprises a varying number of teeth according to the size of the shell. The two series, anterior and posterior, are arranged without disruption beneath the umbo (Pl. 1, fig. 8) and so the teeth are difficult to count.

Length of shell (mm) 3, 3·5, 6·5, 7·5, 7·8, 8·5, 10, 10, 10·5, 12, 12·5, 13, 13·5, 14, 15, 16, 16, 17, 19
Number of posterior teeth 6, 7, 6, 9, 6, 10, 8, 13, 10, 15, 14, 14, 11, 13, 14, 16, 21, 15, 17
Number of anterior teeth 6, 5, 6, 9, 6, 7, 7, 11, 9, 10, 12, 10, 9, 13, 13, 12, 10, 12, 13

Several specimens have more numerous posterior teeth, a character also indicated by Bradshaw, and considered by Tunnicliff as a criterion for the genus *Deceptrix*. However, the umbo is in the posterior half, a character of *Praenucula*.

The anterior teeth are convex, beneath the umbo they are orthomorph, and on the posterior hinge plate they are convexo-concave and concave. A single specimen (RA-I 2167/OR) shows an inconspicuous disruption between the two series.

Discussion. Bradshaw (1970) studied, using material from the Armorican Ordovician, the discrimination of the two Sharpe species, *costae* and *ciae*. *P. costae* shows 'two series of teeth arranged at an angle to each other', also figured by Babin (1966, figs 27 and 28; pl. 2, figs 6, 12, 13) under the designation *Palaeoneilo ctenodontoides* (this generic conception of *Palaeoneilo*, that of Douvillé [1912, p. 38], became outmoded after McAlester's revision in 1968). One of us (C.B.) observed that Sharpe's type of *P. costae* (BMNH, Pl. 4100) shows this disruption. It is only seen in one Spanish specimen (see above); nevertheless the distribution of the teeth, i.e. more numerous in the posterior hinge plate, is close to *P. costae*. Moreover, Bradshaw (1970) wrote "*P. costae* is particularly interesting as it is the more variable of the two species and sometimes exhibits a dental plate similar to that of *P. ciae*". She also figured (text-fig. 10) an internal mould of *P. costae* without the discordance between the two series of teeth.

Another character used by Bradshaw to distinguish between the two species is the pattern of the accessory muscle scars. The umbonal scars are usually preserved and well marked in the Armorican material (Babin 1966, fig. 26; Bradshaw 1970, figs 8, 9, 12), but they are not present or preserved in the Spanish material. On the other hand, the position of the accessory scar lying half-way along the posterior part of the hinge plate is always seen, which, according to Bradshaw, is a feature of *P. costae*. So it seems justified to consider *P. costae* as a polymorphic species and to place the Spanish specimens within it. The variations affecting the dentition and the accessory scars are thus considered dependent on intraspecific variability between geographically isolated populations.

There are other related species of *P. costae* and *P. ciae*; for example, '*Ctenodonta*' *nuda* from the Swedish Middle Ordovician (Soot-Ryen and Soot-Ryen 1960, pl. 1, fig. 1) has a narrower posterior end. It is possible that some of the specimens from Bohemia, illustrated by Barrande (1881, pl 269) as *Leda bohemica*, are closely allied to, if not conspecific with, *P. costae* (Pfab 1934, p. 223, excluded from *C. bohemica* several of Barrande's specimens). Tunnicliff (1982, p. 50) has also compared *P. praetermissa* from the Irish Ashgill with *P. costae* and *P. ciae*. Thus, this palaeotaxodontid morphology was very frequent during the Middle and Upper Ordovician.

Praenucula sharpei n. sp.

Plate 2, figs 1–6

1984*b* *Deceptrix* n. sp. Martin *in* Gutiérrez-Marco *et al.*, p. 302.

Holotype. Internal mould of a right valve showing the dentition, RA-I 2148/OR.

Type locality and horizon. 7500 m ESE from Horcajo de los Montes (Ciudad Real), in the El Calvario hillock peak (646 m), N of Los Rasos de Navalaceite hamlet. Reddish shales with coquinas from the upper half of the Navatrasierra Shales; early Upper Llanvirn (*Cacemia* beds).

Derivation of name. Dedicated to Daniel Sharp who was the first describer of Ordovician bivalves from the Iberian peninsula.

Paratypes. RA-I 2 146/OR, 2 147/OR, 2 149/OR, 2 183/OR; NE-IV 2 189/OR (two specimens); PZ-III 2 187/OR, 2 188/OR (two specimens); RE-IX 2 186/OR; SP-IV 2 184/OR; VPA-2 144/OR, 2 145/OR, 2 185/OR (ten specimens).

Diagnosis. Small species of *Praenucula*, convex and high, with few teeth distributed almost equally between the two parts of the hinge plate. Adductor muscle scars not very extended and badly impressed.

Description and discussion. Shells are generally small (of 32 measured specimens, the mean length is 8·6 mm, the range 4·7–15·5 mm). Anterior region is a little elongated and the posterior one rounded. The umbones lie in the posterior half but near the middle of the length (mean of the umbonal index: 56·04). Shell is high (mean of the lengthening index [C. Babin, 1966]: 75·57). The cardinal side is gently arched. Adductor scars discrete, oval, situated in the anterior and posterior angles; a small pedal posterior scar occurs between the posterior adductor and the hinge plate, and an anterior scar adjacent to the upper point of the anterior adductor muscle.

Dentition usually limited to the middle part of the cardinal line with few teeth (generally about 12, ranging from 7 for a shell 5 mm long to 28 for a shell 15·5 mm long). The teeth are nearly similar in size (the posterior ones are a little smaller in the largest specimens).

This species differs from all those described in the literature in its shape and short dentition, and is known only from Spain.

Genus CARDIOLARIA Munier-Chalmas, 1876

Type species. By original designation, *Cardiolaria barrandei* Munier-Chalmas, 1876, p. 107, from the Upper Ordovician of the Armorican Massif.

From the specimens of the type-species he could examine, McAlester wrote (1968) 'the dentition immediately below the umbo is not preserved'. One of us (C.B.) has found in the collections of the University of Lille some specimens from the type-locality (la Bouëxière) and one of them shows an edentulous space beneath the umbo, between the two series of teeth. This shows it to be attributable to the genus *Cardiolaria*.

Cardiolaria beirensis (Sharpe, 1853)

Plate 3, figs 4–7

1853	*Nucula beirensis* Sharpe, p. 150, pl. 9, figs 11 and 12.
1918	*Nucula beirensis* Sharpe, Born, p. 337.
1970	*Cardiolaria beirensis* (Sharpe), Bradshaw, p. 624, figs 1–4 (see for synonymy).
1978	*Cardiolaria beirensis* (Sharpe), Pojeta, pl. 2, fig. 15.

Material. About 180 internal moulds. The species is common from FB-IV, NE-VII, RA-I, RE-VI and La Vibora.

Localities and stratigraphical range. Late Lower Llanvirn-Upper Llandeilo, relatively scarce in shales but well represented in sandstone facies. The studied samples come from the West Asturian-leonese zone (loc. TR-III, Iberian Cordillera (FB-IV, GA-II) and the Central-Iberian zone (ALAM-IV, CHI-IV-V, CO-XII and XIIIA, FU-IX, HD-IV and VI, La Carcel, La Vibora, NE-VII, PI-III and IV, PSV-III and V, RA-I, RE-VI, SVA-II).

Description and discussion. Shell outline rounded and moderately convex, on the internal moulds with a strong prosogyrous beak. Anterior adductor muscle scar fringed on its internal margin by a strong myophoric buttress; posterior adductor scar little impressed (the accessory scars are not visible except for an anterior pedal scar adjacent to the anterior adductor scar). Dentition comprising five or six anterior teeth and 15 to 20 small posterior teeth. The two series are discordant and separated by an edentulous space below the umbo (Pl. 3, figs 4 and 5) though Bradshaw (1970) noted that juvenile specimens have a continuous dentition. We have observed two very young specimens (FSL 550 094 and FSL 550 095) in the Armorican material with a length of 2 mm and 4·2 mm respectively; their weak adductor scars and dentition are interesting ontogenetically (Text-fig. 4).

It is undoubtedly material of this species from Almadén that de Verneuil and Barrande (1856) determined as *Nucula hopensacki*. Douvillé (1912, p. 439) drew the hinge area, with a wrong age attribution to the Cambrian; his original material appears to have been lost.

We also consider that four small specimens (Pl. 3, fig. 6, 7) from locality RA-I 2 179/OR to RA-I 2 181/OR are possible juvenile forms of *C. beirensis*. Their lengths are 6·5 mm, 6·5 mm, 9 mm, and 10·5 mm. The hinges exhibit a continuous series of 22 to 25 posterior and umbonal teeth (these latter very small) and four or five

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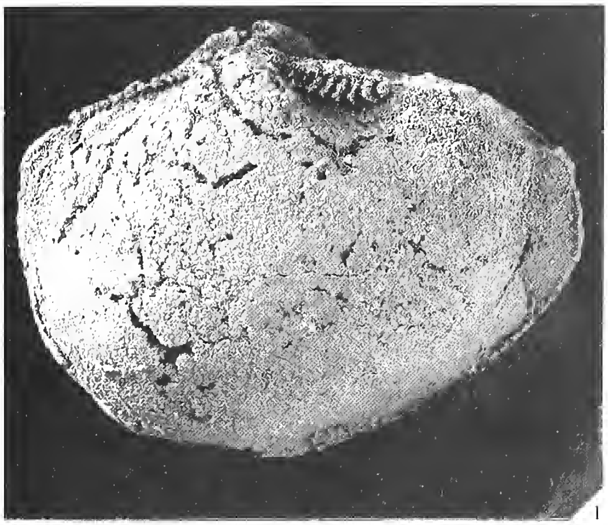
EXPLANATION OF PLATE 2

Figs 1–6. *Praenucula sharpei* n. sp. 1, right view of an internal bivalve mould (VPA 2 144/OR), Ventas con Peña Aguilera (Toledo), lower part of the Navas de Estena Shales, Lower Llanvirn, ×5. 2 and 3, paratypes, Navalpino (Ciudad Real), upper half of the Navatrasierra Shales, early Upper Llanvirn; 2, internal mould of a right valve (RA-I 2 146/OR), ×8; 3, internal mould of a left valve (RA-I 2 149/OR), ×8. 4, internal mould of a left valve from San Pablo de los Montes (Toledo), Lower Llanvirn (SP-IV 2 184/OR), ×8. 5, holotype, same locality as paratypes, internal mould of a right valve (RA-I 2 148/OR), ×8. 6, internal mould of a left valve from Venta con Peña Aguilera (Toledo), Lower Llanvirn, ×5.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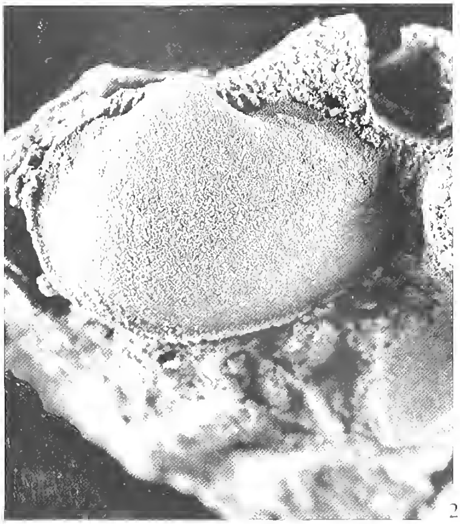
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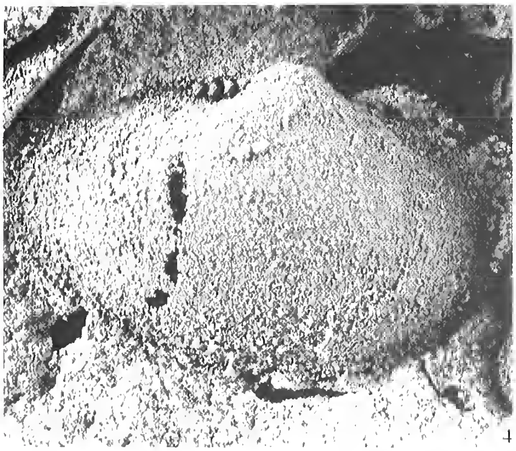
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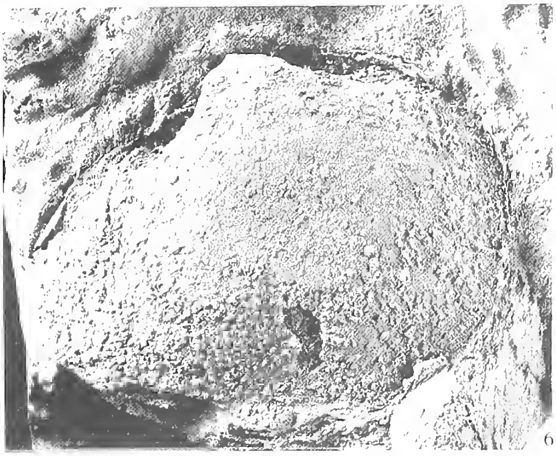
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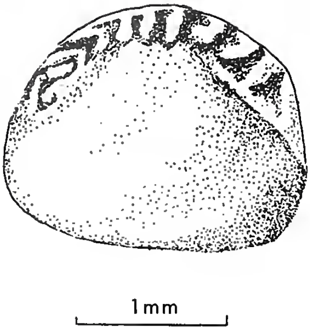
BABIN and GUTIÉRREZ-MARCO, *Praenucula sharpei* n.sp.



TEXT-FIG. 4. *Cardiolaria beirensis* (Sharpe, 1853). Internal mould of the right valve of very young specimen (FSL 550 094) from the Armorican Massif. The beak is broken and the dentition appears continuous.

anterior teeth which are stronger. A very similar arrangement was figured by Bradshaw (1970, fig. 1). However, the Spanish specimens have peculiar muscular impressions. The adductor scars are well developed and there is a strong anterior myophoric plate, but the accessory muscle scars are deeply impressed and numerous. There is a prominent anterior pedal scar adjacent to the posterior adductor; these pedal scars are elongated perpendicular to the cardinal margin. There are three other accessory scars, with one on the posterior slope of the umbonal region and the others in the median region of the valve (Pl. 3, fig. 6, 7). These specimens were determined as *Tancrediopsis ezquerrae* (Sharpe) by Gutiérrez-Marco *et al.* (1984*b*), but they do not have the adductor scars of that species which also possesses larger and fewer posterior teeth. We also note that *T. ezquerrae*, described from Portugal and common in the Armorican Massif, is absent from the observed Spanish material (another bad specimen [RE-VI 2 214/OR] may belong to the genus *Tancrediopsis* but not to the species *T. ezquerrae*). In these small specimens of *C. beirensis* the partition beneath the umbo of the two series of teeth appears late during ontogeny with later resorption; see also Bradshaw (1970). In some forms, the accessory musculature is reduced during ontogeny.

Family TIRONUCULIDAE Babin, 1982
Genus EKATERODONTA Babin, 1982

Type species. By original designation, *Ekaterodonta courtessolei* Babin, 1982, p. 38, from the Arenig of the Montagne Noire (South of France).

Ekaterodonta hesperica n. sp.

Plate 3, figs 1–3

Holotype. Internal mould of a right valve showing the dentition, CR-II 2 152/OR.

EXPLANATION OF PLATE 3

Figs 1–3. *Ekaterodonta hesperica* n. sp. Aragoncillo Massif (Iberian Cordillera), basal part of La Venta Formation, lowermost Llanvirn. 1, holotype, internal mould of a right valve showing the dentition (CR-II 2 152/OR), × 10. 2, paratype, internal mould of a left valve (CR-II 2 154/OR), × 6. 3, paratype, internal mould of a right valve (CR-II 2 153/OR), × 6.

Figs 4–7. *Cardiolaria beirensis* (Sharpe, 1853); 4 and 5, La Vibora, ? Upper Llandeilo, latex replica of two right valves showing the discordant series of teeth (FSL 550 109, FSL 550 110, × 6. 6 and 7, Navalpino (Ciudad Real), upper half of the Navatrasierra Shales, early Upper Llanvirn; 6, internal mould of a left valve showing accessory muscle scars (RA-I 2 179/OR), × 8.5; 7, internal mould of a right valve with accessory scars (RA-I 2 181/OR), × 10.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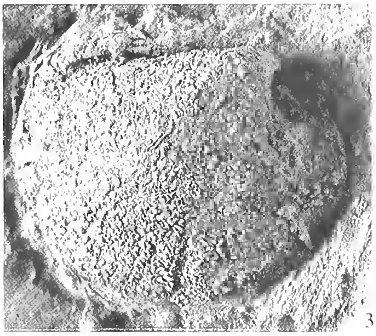
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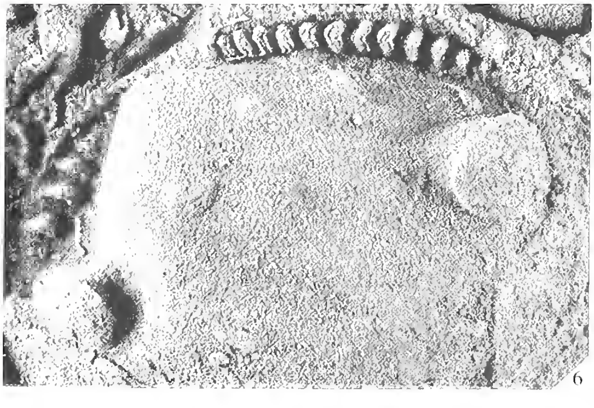
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BABIN and GUTIÉRREZ-MARCO, Middle Ordovician Bivalvia

Type locality and horizon. 2300 m N of Aragoncillo village, and 900 m WNW of Aragoncillo mountain (1518 m), in the talus of the first track to the Canaleja spring. Dark shales of the basal part of La Venta Formation; earliest Lower Llanvirn.

Derivation of name. After the Hesperian Massif, where most of the Ordovician outcrops in the Iberian Peninsula are situated.

Paratypes. Internal moulds CR-II 2 153/OR, CR-II 2 154/OR, CR-II 2 155/OR and CR-II 2 156/OR (6 specimens).

Diagnosis. Shell small, rounded and smooth, with anterior beak; anterior adductor muscle scar small, rounded, faintly impressed; posterior one is indistinct; dentition has two short anterior pseudolateral teeth, some small orthomorphic teeth beneath the umbo and, on the posterior hinge plate, some small chevron-shaped teeth and a large lamellar tooth.

Description and discussion. The shell is small (length range from 6·5 to 11 mm) and high (average lengthening index 84·80 based on 9 specimens); beak is curved and anterior (average umbonal index 26·57); outline rounded anteriorly and ventrally with a slightly truncate posterior end. The dentition is only complete on the holotype; its poor preservation and fragility do not allow a cast to be made. It comprises two short lamellar anterior teeth perpendicular to the anterior margin of the hinge plate and a posterior pseudolateral tooth; the latter possibly corresponds to the extension of the upper arm of an underumbonal tooth and surmounts the 8 or 9 more posterior teeth of the series.

The outline, its ornamentation and particularly its dentition, are very similar to the type species. Nevertheless, this species differs in its weak adductor muscle scars.

Superfamily NUCULANACEA Adams and Adams, 1858
Family MALLETIIDAE Adams and Adams, 1858
Genus MYOPLUSIA Neumayr, 1884

Type species. Leda bilunata Barrande, 1881, by subsequent designation of McAlester, 1968, p. 35.

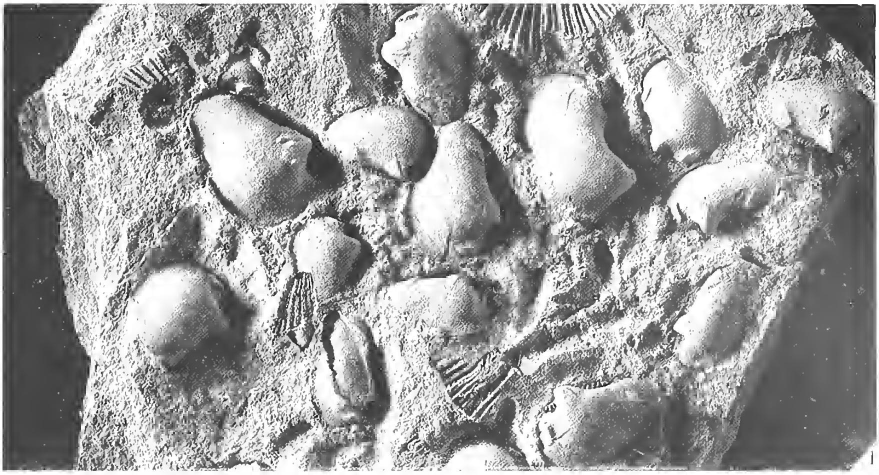
Myoplusia bilunata perdentata (Barrande, 1881)

Plate 4, fig. 1–8

1881 *Leda bilunata* Barrande, pl. 270, I, figs 13–24.
1881 *Leda perdentata* Barrande, pl. 270, II, figs 1–9.
pars 1918 *Leda bohemica* Barrande, Born, p, 338, pl. 24, fig. 5.
1934 *Ctenodonta bilunata perdentata* (Barrande), Pfab, p. 227, pl. 2, figs 12–13.

EXPLANATION OF PLATE 4

Figs 1–7. *Myoplusia bilunata perdentata* (Barrande, 1881) 1, many internal moulds of valves of *Myoplusia* from Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo, × 2.7. 2 and 3, Barrande's specimen (1881, pl. 270, figs 1–4), paratype after McAlester, 1968, Sterboholy (Czekoslovakia), Middle Ordovician, Národní Museum Collections (Prague), left and cardinal views of an internal bivalve mould (phot. J. Kříž), × 7. 4, Barrande's specimen (1881, pl. 270, I, fig. 21–24), cardinal view of a partial bivalve mould (phot. J. Kříž), × 7. 5–7. Calzada de Calatravia (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo; 5, internal mould of a right valve (CC-I 2 131/OR), × 7; 6, latex replica of the dentition of a left valve (CC-I 2 129/OR), × 10; 7, latex replica of a right valve (CC-I 2 176/OR), × 7. 8, Barrande's specimen (1881, pl. 270, II, fig. 7–9), also figured by Pfab (1934, pl. II, fig. 13), Sterboholy (Czekoslovakia), Middle Ordovician Národní Museum Collections (Prague), internal mould of a right valve (phot. J. Križ), × 5.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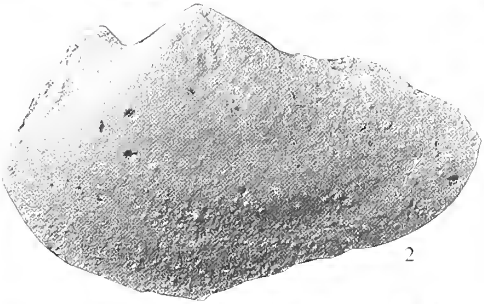
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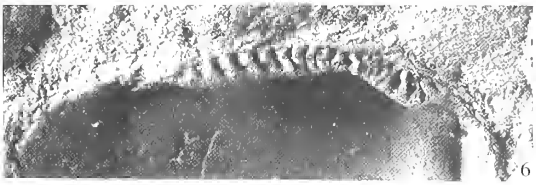
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BABIN and GUTIÉRREZ-MARCO, *Myoplusia bilunata perdentata*

?1939 *Ctenodonta* (*C.*) *bilunata perdentata* Pfab [sic], Maillieux, p. 33, pl. 2, figs 19–22.
1966 *Ctenodonta* sp., Babin, p. 299, pl. 1, fig. 8.
1972 *Myoplusia* cf. *bilunata perdentata* (Barrande), Babin and Mélou, p. 85, pl. 7, figs 1 and 2.
1973 *Myoplusia* cf. *bilunata perdentata* (Barrande), Babin and Robardet, p. 31, pl. 2, figs 1–6.

Material. Seventy-nine internal and some external moulds.

Localities and stratigraphical range. Upper Llanvirn-Upper Llandeilo (Spanish record of the species); muddy and sandy facies from the Iberian Cordillera (GA-II) and the Central-Iberian zone (ALAM-III, Albadalejo, CC-I, PSV-IV, PZ-III, RA-I, RA-IV, RE-VII).

Description and discussion. Shell always small, length less than 10 mm (average for the Spanish material 6·9 mm). Cardinal margin convex, anterior side weakly truncate; pallial edge widely convex in anterior part (greatest height below the beak), then there is a faint inflexion and the elongate posterior end is less high than the anterior one. Beak prosogyrous, situated towards the anterior third of cardinal line, on internal moulds acute and bent. Adductor muscle scars strongly impressed. Anterior scar oval, perpendicular to cardinal plate; posterior one with anterior linear side inclined almost to the hinge line, and a rounded posterior side. The accessory scars comprise a scar occurring above the posterior adductor.

Dentition paleotaxodont, number of teeth variable (16–30) according to size of the shell. Anterior teeth slightly convex; teeth beneath umbo thin and orthomorph; some concavo-convex teeth follow them without discontinuity from the concave posterior teeth.

Pfab (1934) reduced the contemporaneous species of Barrande (*bilunata* and *perdentata*) to the rank of varieties of the single species *bilunata*. The Spanish specimens belong, without doubt, to the species *bilunata* but it is difficult to assign them to either subspecies. They have the anterior end slightly truncated as in *bilunata bilunata* and the umbonal scars also point to this subspecies. But the narrower posterior end suggests *bilunata perdentata*, which also sometimes has the faintly sinuous pallial margin of the Spanish specimens (we are indebted to Dr J. Kříž for photographs of the specimen figured by Barrande 1881, pl. 270, I, figs 7–9 and by Pfab 1934, pl. 2, fig. 13, showing this morphology; see Pl. 4, fig. 8). Finally, the hinge with the particularly concave posterior teeth is similar to the type figured by Pfab (pl. 1, fig. 5*a*) as *M. bilunata perdentata*. We therefore refer our material to *M. bilunata perdentata*. To exclude it would create another geographic subspecies with some characters of each Bohemian subspecies. Direct comparison with the Armorican material shows that they are very similar, with but tiny differences such as in the position of the posterior adductor muscle scar.

Genus CADOMIA Tromelin, 1877

Type species. By monotypy *Cadomia typa* Tromelin, 1877, p. 48; fig *in* Bigot, 1890, pl. 23, fig. 3.

Cadomia britannica (Babin, 1966)

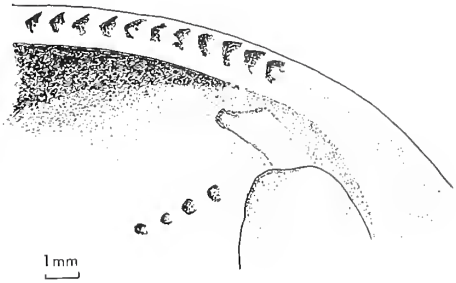
Plate 5, fig. 2

1966 *Ctenodonta britannica* Babin, p. 54, pl. 1, fig. 1
1984*b* *Deceptrix* ? *britannica* (Babin), Gutiérrez-Marco *et al.*, p. 302.

Material. Ten external moulds of right and left valves.

Localities and stratigraphical range. This rare species is known only from six localities in the southern part of the Central-Iberian zone (CHI-IV, Fontanosas, HD-VI, NE-VII, PI-III and SEU-II); muddy facies close to the Llanvirn-Llandeilo boundary.

Description and discussion. All the valves are large (length, 30–40 mm); the outline is oval with the beak in the anterior third of the shell. Dentition with a continuous series of teeth; 6–8 anterior teeth convex, 6–7 teeth beneath the umbo orthomorph, 25–30 posterior teeth convex. Adductor muscle scars clearly marked, oval, but not very large; accessory scars with a pedal anterior one, situated behind the dorsal extremity of the anterior adductor, and a pedal posterior one in contact with the dorsal margin of the posterior adductor. Another pronounced scar near the hinge plate, half-way between the posterior adductor and the umbo. Several small scars situated on the anterior side of the umbonal cavity; lastly, four tiny scars (?) seem to precede the posterior adductor (Text-fig. 5). The Spanish specimens are identical with those from the Armorican Massif (Babin 1966). Generic attribution is difficult; we tentatively assign this species to *Cadomia* because it is an inequilateral shell with numerous taxodont teeth without disruption beneath the umbo. This species is not very common and seems to be restricted to the basal Llandeilo.



TEXT-FIG. 5. *Cadomia britannica* (Babin, 1966). Upper posterior region of a latex replica (CH-I-V 2 143/OR) showing four minute muscle scars in front of the posterior adductor.

Subclass ISOFILIBRANCHIA Iredale, 1939
Order MODIOMORPHOIDA Newell, 1969
Superfamily MODIOMORPHACEA Miller, 1877
Family MODIOMORPHIDAE Miller, 1877
Genus GONIOPHORA Phillips, 1848
Subgenus COSMOGONIOPHORA McLearn, 1918

Type species. *Goniophora bellula* Billings, 1874.

Goniophora (*Cosmogoniophora*) sp.

Plate 5, figs 3 and 4

Material. Twenty-five internal and some external moulds of right and left valves.

Locality and stratigraphical range. Recorded only from the basal beds of the La Venta Formation, locality CR-II in the Iberian Cordillera; earliest Lower Llanvirn.

Description and discussion. Small shell (the length of the complete specimens varies from 13 to 22 mm), moderately convex, with a weak umbo and the typical outline of *Goniophora*, i.e. with an elongate postero-ventral angle into which leads a strong carina proceeding from the beak. Ornamentation of fine concentric striae in front of the carina, but of radial costae on the slope behind the carina. Hinge unknown. No muscle scar observable. With its radial costae, this form can be assigned to the subgenus *Cosmogoniophora* but no specific name can be proposed. The genus is known from the Lower Ordovician to the Devonian.

Genus MODIOLOPSIS Hall, 1847

Type species. *Pterinea modiolaris* Conrad, 1838.

Modiolopsis? elegantulus Sharpe, 1853

Plate 5, fig. 1

1853 *Modiolopsis elegantulus* Sharpe, p. 152, pl. 9, fig. 15.

Material. Forty-four internal and some external moulds of right and left valves.

Localities and stratigraphical range. Upper Llanvirn to Upper Llandeilo (muddy facies only) from the Iberian Cordillera (HERR-I, LU-II) and the Central-Iberian zone (AM-I, HD-X, PR-IX, PZ-III, RA-I, III and VI B, RE-IX and IX B).

Description and discussion. Inequilateral valves with rectilinear cardinal hinge; beak, situated between the middle and the anterior third and slightly projected. Greatest height just exceeding the cardinal length. This height, extending from the beak to the postero-ventral part, coincides with the greatest convexity of the shell. Anterocardinal angle rounded; posterocardinal angle obtuse (about 130°). Shell very thin and internal moulds showing clearly the ornamentation of concentric undulations. Hinge apparently edentulous with a short ligament groove behind the beak (?). No muscle scar visible.

The material is poor and does not allow straightforward generic attribution. The morphology, the ornamentation and the edentulous hinge can be as easily compared with *Modiolopsis* among the Modiomorphidae as with some Posidoniidae. The species *elegantulus* was described by Sharpe (1853) based on a single specimen from the Ordovician of Portugal and is probably conspecific with the Spanish material.

Subclass PTERIOMORPHIA Beurlen, 1944
Order ARCOIDA Stoliczka, 1871
Superfamily CYRTODONTACEA Ulrich, 1894
Family CYRTODONTIDAE Ulrich, 1890
Genus CYRTODONTULA Tomlin, 1931

Type species. Whitella obliquata Ulrich, 1890.

Cyrtodontula sp.

Plate 5, figs 6 and 7

Material. A bivalve mould (CHI-V 2 142/OR) and a partially complete specimen.

Localities and stratigraphical range. Llanvirn-Llandeilo boundary; very rare in the Central-Iberian zone (CHI-V and PI-III)

Description and discussion. The badly preserved specimen is strongly inflated and very inequilateral with beaks near the anterior margin. On this internal mould some preserved fragments of the shell show that a clear ornament is superposed on the concentric striae (Pl. 5, fig. 6). The dorsal margin is partially broken behind the beak but the general morphology is very similar to that of many cyrtodontids (*Cyrtodontula*, *Vanuxemia*) or

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EXPLANATION OF PLATE 5

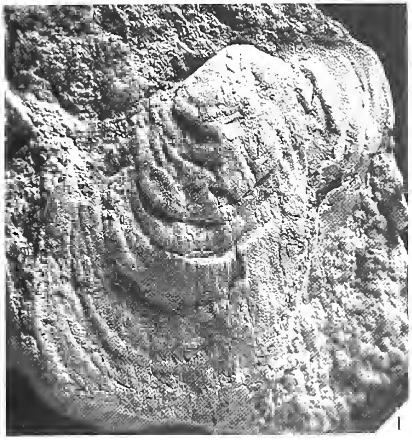
Fig. 1. *Modiolopsis ? elegantulus* Sharpe, 1853. Pozuelos de Calatrava (Ciudad Real), Valdemorillo Shales, Upper Llandeilo, internal mould of a right valve (PZ-III 2 151/OR), ×4.

Fig. 2. *Cadomia britannica* (Babin, 1966). Chillón (Ciudad Real), upper half of the Rio Shales, early Upper Llanvirn, internal mould of a right valve (CH-I-IV, 2 143/OR), ×1.8.

Figs 3 and 4. *Goniophora* (*Cosmogoniophora*) sp. Aragoncillo (Guadalajara), basal beds of La Venta Formation, earliest Lower Llanvirn. 3, partial internal mould of a left valve (CR-II 2 163/OR), ×3. 4, internal mould of a right valve (CR-II 2 162/OR), ×5.

Fig. 5. *Babinka prima* Barrande, 1881. Navas de Estena (Ciudad Real), lower third of the Navas de Estena Shales, Lower Llanvirn, internal mould of an elongate specimen (NE-III 2 128/OR), ×2.

Figs 6 and 7. *Cyrtodontula* sp. Chillón (Ciudad Real), upper half of the Rio Shales, Llanvirn/Llandeilo boundary, left and anterior views of an internal bivalve mould (CH-I-IV 2 142/OR), ×2.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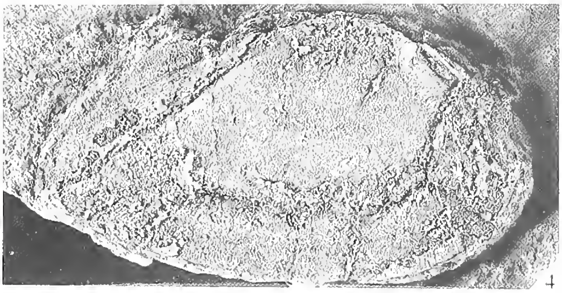
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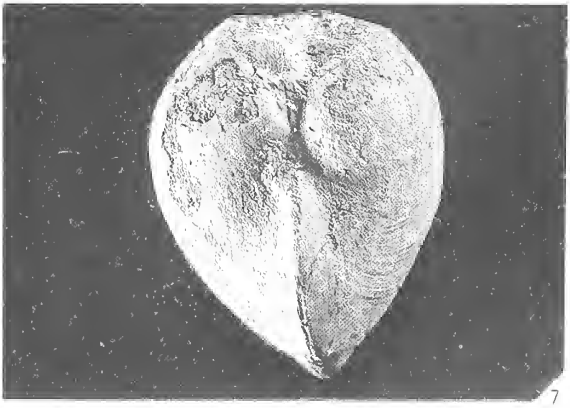
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BABIN and GUTIÉRREZ-MARCO, Middle Ordovician Bivalvia

some modiomorphids like *Plethocardia*. The absence of data concerning the hinge area makes precise generic attribution difficult. However, the apparent absence of a marked anterior adductor scar indicates tentative inclusion within *Cyrtodontula*. De Verneuil and Barrande (1856, p. 990, pl. 27, fig. 5) erected *Cucullaea caravantesi* for a gibbous shell from the Puebla de Don Rodrigo area which might be the same, in spite of a longer postumbonal cardinal part; however we have not found it in de Verneuil's collections. The morphology of this bivalve suggests an endobyssate mode of life as proposed by Frey (1980) for *Vanuxemia*. The genus *Cyrtodontula* is cited from the Upper Ordovician in North America (Richmondian) and in the Baltic area (Isberg 1934), from the Middle Ordovician of Norway (Soot-Ryen and Soot-Ryen 1960), and the 'first records of the genus from the Southern Hemisphere' were given by Pojeta and Gilbert-Tomlinson (1977) from the Arenigian and Trentonian (= late Middle Ordovician?) of Australia.

Subclass HETEROCONCHIA Hertwig, 1895
Order ACTINODONTOIDA Douvillé, 1912
Family CYCLOCONCHIDAE Ulrich, 1894

The diagnosis of the family given by Pojeta and Gilbert-Tomlinson (1977) is 'actinodontids with numerous elongate teeth with lack of denticles'. The species described below, *Glyptarca ? lusitanica*, has microcrenulate teeth and its attribution to this family may therefore be debateable. However, the family Lyrodesmatidae with crenulate teeth is characterized, by the same authors, by 'teeth radiating ventrally from immediately below the beak' and is less appropriate. Thus, we consider that *Glyptarca*? can indeed be considered as a member of Cycloconchidae; the diagnosis of the family should therefore be extended to include the possible presence of denticles on the teeth. In the description of the dentition, we use the terminology pseudocardinals and pseudolaterals proposed by Pojeta and Runnegar (1985, p. 320).

Genus GLYPTARCA Hicks, 1873

Type species. *Glyptarca primaeva* Hicks, 1873 by subsequent designation of Carter, 1971, p. 258.

Glyptarca ? lusitanica (Sharpe, 1853)

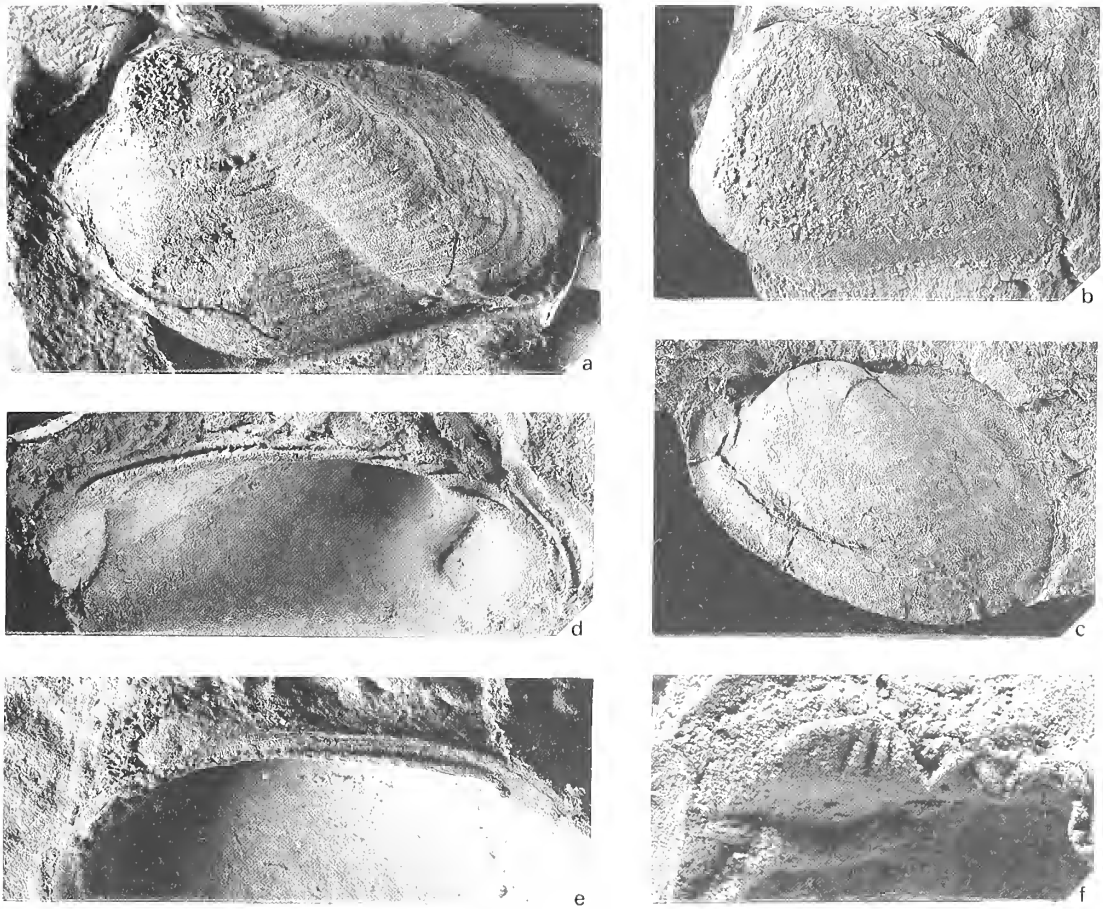
Text-fig. 6

1853	*Dolabra ? lusitanica* Sharpe, p. 151, pl. 9, fig. 3.
?1853	*Cypricardia ? beirensis* Sharpe, p. 152, pl. 9, fig. 16.
1856	*Arca naranjoana* de Verneuil and Barrande, p. 989, pl. 26, fig. 12.
1912	*Actinodonta acuta* Barrois, Douvillé, p. 440, fig. 12 (non Barrois, 1891).
1918	*Modiolopsis ? lusitanica* (Sharpe), Born, p. 342.
1966	*Actinodonta naranjoana* (de Verneuil and Barrande) Babin, p. 233, pl. 10, figs 5, 7, 11. See for synonymy; add:
1970	*Actinodonta naranjoana* (de Verneuil and Barrande) Bradshaw, p. 636, text-figs 13–15.
1978	*Glyptarca naranjoana* (de Verneuil and Barrande), Morris, pl. 1, fig. 2.
1984	*Glyptarca naranjoana* (de Verneuil and Barrande), Gutiérrez-Marco *et al.*, p. 302.
1985	*Glyptarca ? naranjoana* (de Verneuil and Barrande), Babin & Gutiérrez-Marco, fig. 4.

Material. About 280 specimens. The species is particularly common at VPA, NE-VII, la Vibora, CC-I, RA-I and FB-IV.

Localities and stratigraphical range. Widely distributed in the Llanvirn and Llandeilo shales and sandstones of the Hesperian Massif from the West-Asturian-leonese area (TR-III), Iberian Cordillera (FB-I, FB-IV, LU-II, PO-I) and 38 localities in the Central-Iberian zone (AC-I-III) Albadalejo, CC-I and II, CHI-IV, CO-XII, XIII A, XIV-XVI, FU-IX, HO-IV, LB-I, la Carcel, la Vibora, NE-IV and VII, PI-II-IV and IX, PR-IX, PSU-II-III and V, PZ-III, RA-I, I A and IV B, RE-VI and VII, SEU-II, SP-IV, SVA-II, VM-I, VPA).

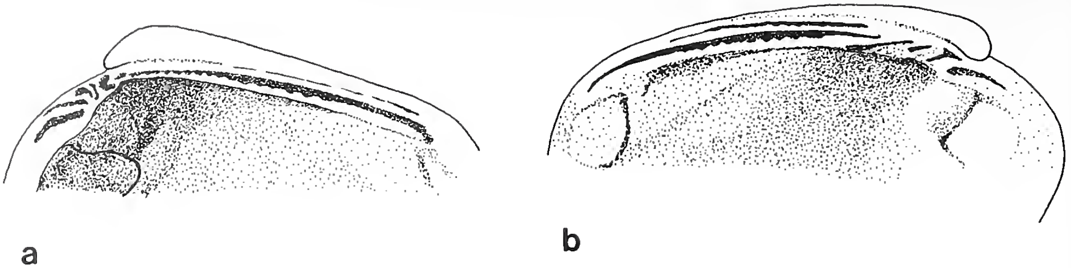
Description and discussion. Shell equivalve, inequilateral, more or less convex; outline slightly variable with subparallel cardinal and ventral margins and a more or less truncate posterior side; ornamentation of fine



TEXT-FIG. 6. *Glyptarca ? lusitanica* (Sharpe, 1853). *a*, *c*. Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo; *a*, left view of a latex replica of an external bivalve mould showing the ornamentation (CC-I 2 175/OR), × 3; *c*, internal mould of an atypical left valve (CC-I 2 175/OR), × 3. *b*, Alia (Cáceres), middle part of the Navas de Estena Shales, early Upper Llanvirn; internal mould of a left valve (PSV-III 2 176/OR), × 3. *d*, Corral de Calatrava (Ciudad Real), middle part of the Alisedas Shales, late Lower Llanvirn; latex replica of the dentition of a left valve (CO-XV 2 132/OR), × 3.3. *e*, Calzada de Calatrava (Ciudad Real), Guindo Shales, late Lower Llandeilo; latex replica of a right valve showing the dentition with the two short anterior pseudolateral teeth, the small pseudocardinals, the elongate and microcrenulated posterior pseudolateral (CC-I 2 209/OR and CC-I 2 140/OR), × 3.3. *f*, Retuarta de Bullaque (Ciudad Real), Navas de Estena Shales, Upper Llanvirn; latex replica showing the microcrenulations of an anterior pseudolateral tooth (RE-IV 2 137/OR), × 10.

concentric striae (Text-fig. 6*a*); blunt carina extending from the beak to the posteroventral angle. Two adductor muscle scars variably impressed, large and round. Accessory muscle scars varying. Bradshaw (1970, fig. 13) figured seven scars which are often not visible; on the other hand, we have observed minute scars posteriorly adjacent to the anterior adductor scar, perhaps corresponding, to labial palps muscles.

Dentition very characteristic. Right valve (Text-figs 6*e* and 7*a*; see also Babin and Gutiérrez-Marco 1985, fig. 4), with two short, lamellar anterior pseudolaterals; the more anterior parallel to the hinge place edge, the second oblique; below the beak, two pseudocardinals variably flexed; the latter is overlapped by an elongate posterior pseudolateral with microcrenulations on two-thirds or three-quarters of its length. The anterior tooth of one specimen has peculiar crenulations on its ventral face (Text-fig. 6*f*). Left valve (Text-figs 6*d* and 7*b*)



TEXT-FIG. 7. *Glyptarca ? lusitanica*, diagrams of dentition. *a*, right valve. *b*, left valve.

showing two microcrenulate posterior pseudolaterals which are often strongly marked and which were considered at one stage as taxodont teeth: 'a long posterior plate parallel to the hinge line, which is *crossed by numerous small teeth or crenulations*' (Sharpe 1853); 'charnière pourvue *de petites dents placées en ligne droite*' (de Verneuil and Barrande 1856) [our emphasis]. Opisthodetic ligament placed in a fine groove.

This Ordovician material is often distorted or flattened, the morphology of the shell is variable, for example in the accentuation of the carina. Nonetheless, there is no reason to distinguish several species. *Cypricardia ? beirensis* Sharpe (1953) that de Verneuil and Barrande (1956) also distinguished, without a figure, also probably belongs to the same species (some specimens from Sharpe's locality, Ribo de Baixo, suggest this is likely). Delgado (1908) made use of the three designations *Dolabra ? lusitanica*, *Cypricardia ? beirensis*, and *Arca naranjoana* without any figures. Born (1918) pointed out that a form from Bohemia, designated *Modiolopsis veterana* by Barrande (1881, pl. 259, III) has some similarities to the present species.

The species *Arca naranjoana* de Verneuil and Barrande, 1856 (= *Dolabra ? lusitanica* Sharpe, 1853) was tentatively attributed to the genus *Actinodonta* by Babin (1966) and Bradshaw (1970), and later to *Glyptarca* (Morris 1978). In fact, this species differs from *Actinodonta* (and from *Cycloconcha*) which have more numerous teeth with anterior pseudolaterals, radiating more regularly from below the umbo: these genera do not have microcrenulations on the teeth. Morris (1978) employed the generic designation *Davidia* Hicks, 1873 for the Ordovician species *ramsayensis* (Hicks 1873) and *carinata* (Barrois 1891). Nevertheless, Carter (1971) pointed out that the type species *Davidia ornata* Hicks is unusable and placed it tentatively in synonymy with *Actinodonta ramsayensis* whose dentition is poorly known. In the same way, *Actinodonta carinata* Barrois does not provide clear information with regard to the dentition beneath the umbo (Babin 1966). So, the use of *Davidia* would require further investigation. Lastly, *Glyptarca* is a poorly defined genus (Carter 1971) with a small edentulous space between the anterior and posterior teeth (Morris 1978; Pojeta 1985). The Spanish species does not present a similar space in the dentition (Text-fig. 7) and we refer it to *Glyptarca* with a query.

Glyptarca ? lusitanica is very common in the Iberian Peninsula and the Armorican Massif. Morris (1978, pl. 1, fig. 2) has figured a specimen from Shropshire and Fortey and Morris (1982) indicate the presence of *Glyptarca* cf. *naranjoana* from the Hanadir Shales (Llanvirn) in Saudi Arabia.

Genus ANANTERODONTA Babin and Gutiérrez-Marco, 1985

Ananterodonta oretanica Babin and Gutiérrez-Marco, 1985

Text-fig. 9*f*

This species has recently been described on the basis of a single specimen from the Lower Llanvirn of San Pablo de los Montes (Toledo). Its phylogenetic significance is considered below.

Family BABINKIDAE Horný, 1960

Genus BABINKA Barrande, 1881

Babinka prima Barrande, 1881

Plate 5, fig. 5

Spanish material of this species has recently been revised by Gutiérrez-Marco and Babin (1988); it is only cited and illustrated here. Its geographic distribution is discussed below.

?Family COXICONCHIDAE Babin, 1977
Genus COXICONCHA Babin, 1966

Coxiconcha britannica (Rouault, 1851)

This species was revised by Babin (1977), who proposed a subfamily Coxiconchinae within the Modiomorphidae. According to Pojeta and Runnegar (1985), the family belongs, in the subclass Isofilibranchia, with Babinkidae placed amongst the Heteroconchia. If so, it also seems justified to place *Coxiconcha* here because of its relations with *Babinka*.

C. britannica is very common (584 specimens were collected) in Llanvirn shales and locally also in the early Lower Llandeilo beds. After its disappearance in the muddy facies in younger beds of the Llandeilo, the last record of the species seems to be from the Upper Llandeilo sandy facies (only from ALAM-IV). The studied material comes mainly from 34 localities in the Central-Iberian zone (AC-I, ALAM-III and IV, Albadalejo, CHI-I, IV and V, CO-X, XII and XII A, FU-IX, HD-I, VI and VII, HM-I, IV and V, NE-III-VII, PI-II, III and IX, PS-III, RA-I, I A and I B, RE-II, SEU-II, SP-IV, VM-I, VPA) with only one locality in the West Asturian-leonese zone (TR-III).

Family REDONIIDAE Babin, 1966

Diagnosis. Is here emended to include the new genus *Dulcineaia* (see below). Very inequilateral actinodontoids with anterior and recumbent beaks; a high myophoric buttress limits the anterior adductor muscle posteriorly; hinge plate bearing one or two short pseudocardinal teeth and one or two elongate posterior pseudolaterals; teeth smooth or microcrenulated.

Genus REDONIA Rouault, 1851

Type species. Redonia deshayesiana Rouault, 1851, p. 364.

Diagnosis. Redoniidae with smooth teeth and chevron-flexed pseudocardinals.

Remarks. Redonia is very common in the southern part of the Gondwanan shelf, and the Spanish material is significant in producing new information leading to its redescription. Unfortunately, the original description (with a misorientation) and illustrations given by Rouault are not very informative and the original material is apparently lost. In the collections of the University of Rennes, there are some very poor specimens, possibly from Rouault's collections but not those figured by him; they come from Gahard (north of Rennes), a locality cited by Rouault, and from Guichen (south of Rennes). From the collections of the Muséum National d'Histoire Naturelle (Paris), we have examined three specimens from localities in Loire-Atlantique (south of the Armorican Massif) none of which is Rouault's material. In the University of Lyon, Verneuil's collections contain specimens from Riadan (south of Rennes) from Vitré (another locality cited by Rouault) and from Brix (Manche). In all these collections, the specimens are labelled *R. deshayesiana* or *R. duvaliana* without discriminating characters. We believe that the descriptions and drawings of Rouault refer to a single species, based on material from Gahard. The present revision requires the designation of a neotype for *R. deshayesi.* The material from the localities near Rennes is badly preserved and its age is not precisely known. Therefore, we select a neotype from the equivalent Postolonnec Formation in the western part of the Armorican Massif (see below).

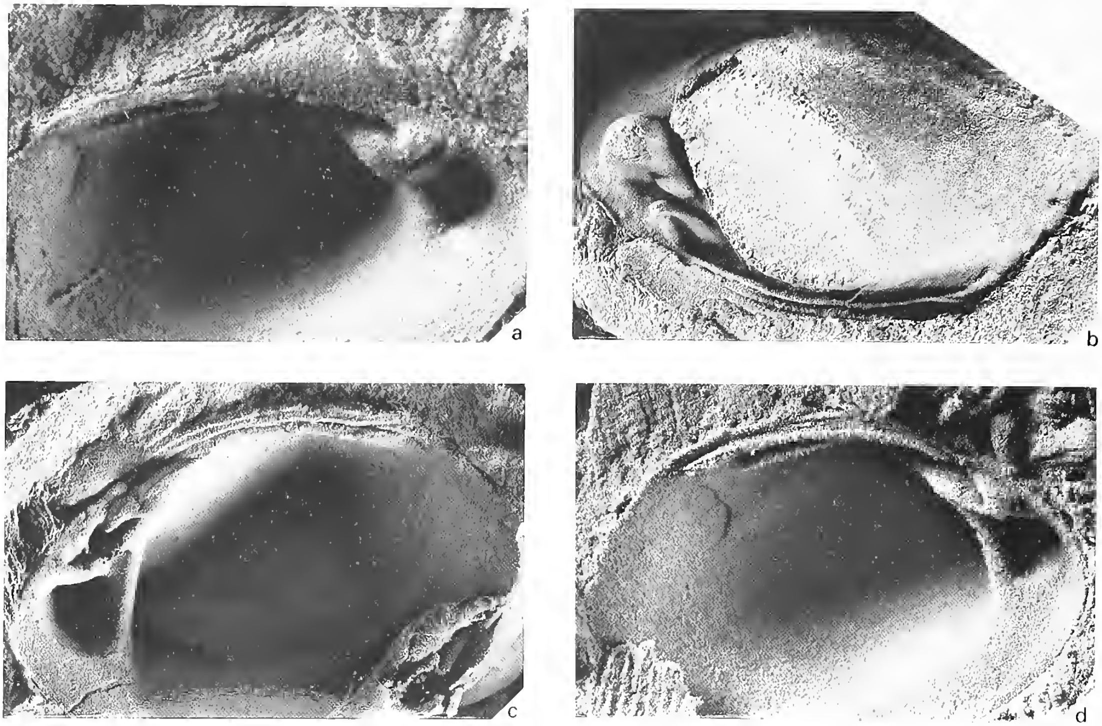
Redonia deshayesi Rouault, 1851

Plate 6, figs 1–7; Text-figs 8 and 9

Synonymy. See Babin 1966, p. 246. Add:

1881 *Redonia bohemica* Barrande, pl. 268, figs 1–26.
1918 *Redonia deshayesiana* Rouault, Born, p. 339, pl. 25, fig. 1*a–f.*
1918 *Redonia deshayesiana* var. *duvaliana* Rouault, Born, p. 341, pl. 25, figs 2*a–f.*
1950 *Redonia deshayesi* Roemer em. Borneman (sic!), Termier and Termier, pl. 163, fig. 2.
1950 *Redonia bohemica* Barrande, Termier and Termier, p. 87, pl. 165, figs 1–3, 6–9.
1950 *Redonia megalodontoides* Termier and Termier, p. 87, pl. 165, figs 4 and 5.
1951 *Redonia deshayesiana* Rouault em. Born, Gigout, p. 296, pl. 2, fig. 14.

1970 *Redonia deshayesi* Rouault, Bradshaw, p. 638, text-figs 16–21.
1978 *Redonia bohemica* Barrande, Pojeta, pl. 4, figs 1–4.
non 1978 *Redonia deshayesiana* Rouault, Pojeta, pl. 4, fig. 5 (= *Dulcineaia manchegana* n.g., n.sp.).
1984*a* *Redonia deshayesi* Rouault forma α, Gutiérrez-Marco *et al.*, p. 302.
1984*b* *Redonia* cf. *deshayesi* Rouault, Gutiérrez-Marco *et al.*, p. 19, pl. 1, figs 13 and 14.

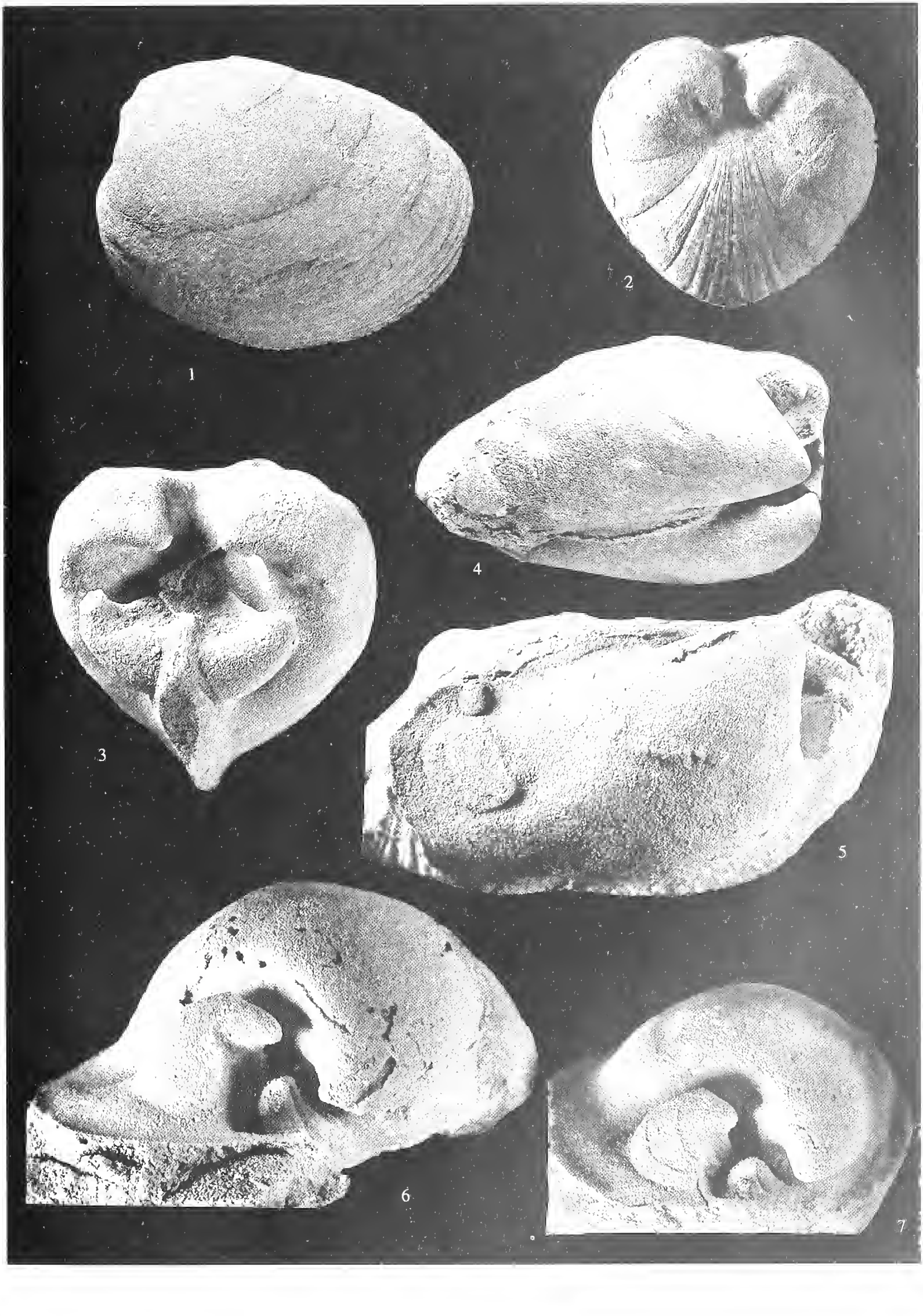


TEXT-FIG. 8. *Redonia deshayesi* Rouault, 1851. Some aspects of the dentition. *a*, latex replica of the left valve of a young specimen (CC-I 2 100/OR), ×12. *b*, dorsal view of the internal mould of the anterior adductor muscle and of the cardinal tooth of a right valve (CC-I 2 087/OR), ×5. *c*, latex replica of the right valve of figure *b*, ×5. *d*, latex replica of the cardinal region of a left valve (RA-I 2 112/OR), ×5.

EXPLANATION OF PLATE 6

Figs 1–7. *Redonia deshayesi* Rouault, 1851. 1 and 2, Luciana (Ciudad Real), middle third of the Navas de Estena Shales, Lower Llanvirn, left and anterior views of a bivalve specimen showing the ornamentation (PI-III 2 125/OR), ×3. 3–7, Navalpino (Ciudad Real), upper half of the Navatrasierra Shales, early Upper Llanvirn; 3, anterior view of an internal mould showing two minuscule muscle scars on the anterior part of the left umbonal region (RA-I 2 115^{bis}/OR), ×5; 4, laterocardinal view of an internal bivalve mould showing elongate muscle scars on the umbonal region (RA-I 2 113/OR), ×3.5; 5, internal mould of a right valve showing united small accessory muscle scars (RA-I 2 115/OR), ×5; 6, anterior view of an internal mould of a right valve showing the shapes of the anterior adductor and the anterior tooth (RA-I 2 120/OR), ×6; 7, anterior view of an internal mould of a right valve showing the same morphology and growth lines on the adductor pillar (RA-I 2 117/OR), ×6.

PLATE 6

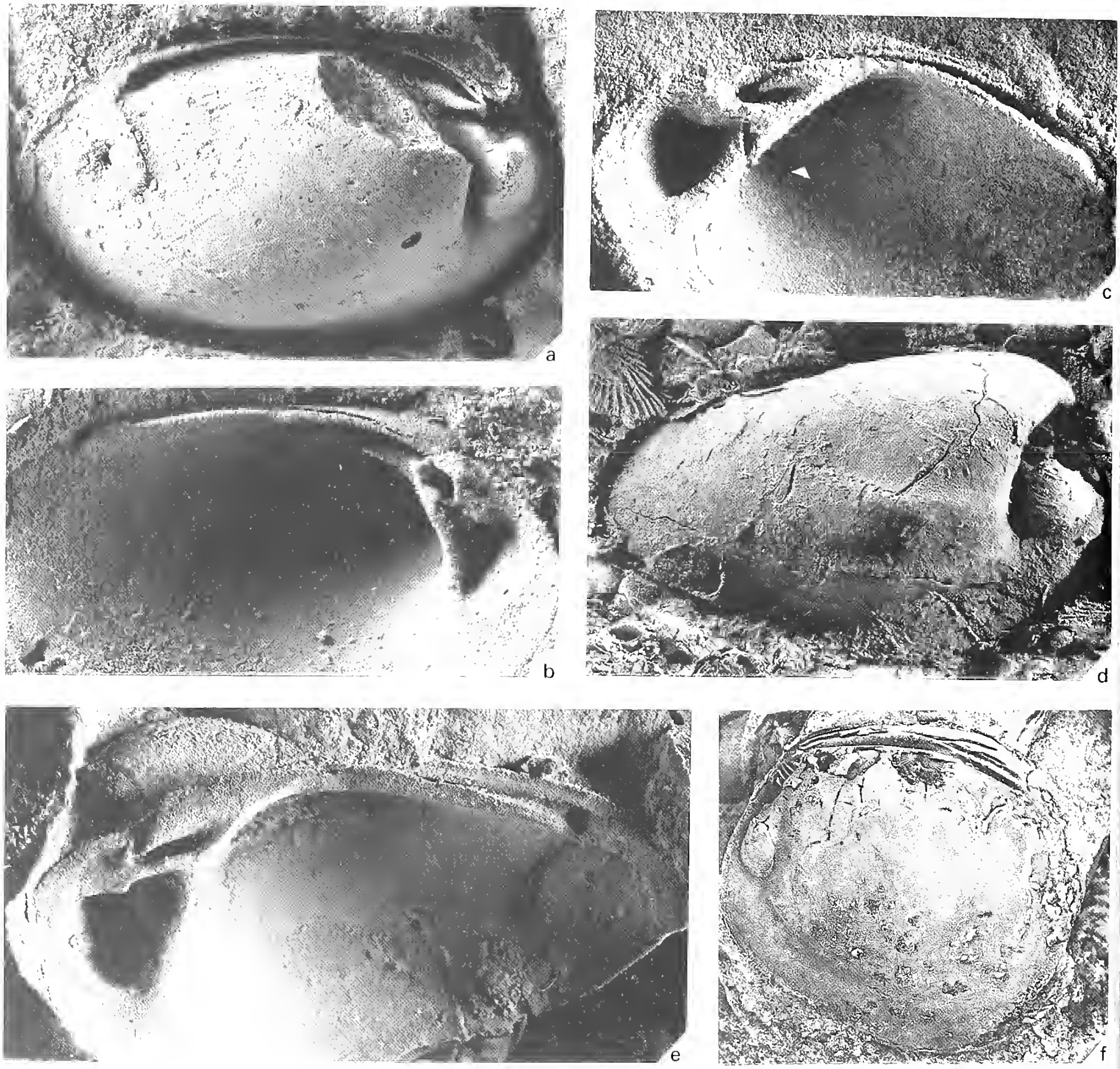


BABIN and GUTIÉRREZ-MARCO, *Redonia deshayesi*

Neotype. LPB 796 (Laboratoire de Paléontologie de Brest). An internal mould of a right valve; Postolonnec Formation. Locality Morgat by Crozon (Finistère, France). Llandeilo (Text-fig. 9*d*).

Material. 825 specimens.

Localities and stratigraphical range. The species is very abundant and reaches a broad distribution (Lower Llanvirn to Upper Llandeilo) in the Tristani beds of the Cantabrian zone (Sueve), West Asturian-leonense zone



TEXT-FIG. 9. *Redonia deshayesi* Rouault, 1851. Some specimens from other countries. *a*, internal mould of a right valve from Wosek (Bohemia) (FSL 550 120), × 5. *b*, latex replica of a left valve from Postolonnec (Finistère, Armorican Massif) (FSL 550 084), × 8. *c*, latex replica of the right valve of figure *a*, × 5. *d*, neotype, internal mould of a right valve, Postolonnec Formation (Llandeilo), Morgat near Crozon (Finistère, Armorican Massif) (LPB 796), × 4. *e*, latex replica of a right valve from Brix (Armorican Massif), Llandeilo (FSL 550 120), × 5. *f*, *Ananterodonta oretanica* Babin and Gutiérrez-Marco, 1985. Holotype and only known specimen, internal mould of a left valve, San Pablo de los Montes (Toledo), Lower Llanvirn (SP-IV 2 073/OR), × 2.

(TR-III), Iberian Cordillera (CA-II, CR-II, FB-I and IV, HERR-I, PS-I, PO-I), Central Iberian zone (AC-I, ALAM-III, CC-I and III, CHI-I, IV and V, CO-XII and XIV, GS-III, HD-IV-VII, HM-I and IV, LB-I, NE-III-VII, PC-I, PI-II-IV and IX, PSV-II-V, RA-I-VI, RE-IX, SEU-II, SP-IV, SVA-II, VM-I, VPA) and Ossa Morena zone (CS-IV).

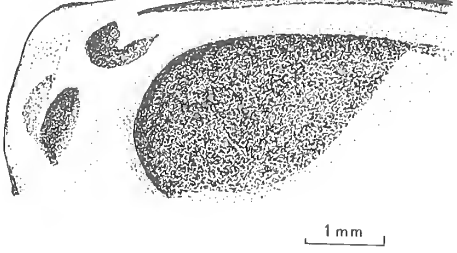
Description and discussion. Shell equivalve, strongly inflated and very inequilateral with the umbo anterior and bent on the cardinal line. Ornamentation concentric with some grooves of growth more marked than others (Pl. 6, figs 1 and 2); these may correspond to stasis of annual growth; according to this hypothesis, specimens such as PI-II 2125/OR show that the shell could reach a length of 10 mm during the first year and had slow growth subsequent to the third year.

Anterior adductor muscle scar very strongly and deeply impressed with a myophoric plate. Some accessory muscle scars present. A pedal retractor adjacent to the posterior adductor scar; another situated at the internal basis of the anterior adductor (Bradshaw 1970 showed that it corresponds to the fusion of two initially more or less distinct scars). Further accessory scars sometimes visible in the umbonal region. Bradshaw (1970, text-figs 16–20) noted the frequent presence of two scars in this position. In the Spanish material, we can see that these small accessory scars vary in number and shape as is to be expected of individual or populational variation. Specimens from locality RA-I provide good examples of such variability. Some have four small scars which are sometimes united into a single elongate scar (Pl. 6, fig. 5) or which remain separate with an elongate shape directed towards the umbo (Pl. 6, fig 4). One specimen shows in addition two minute scars on the anterior portion of the umbo region (Pl. 6, fig. 3). Pallial line entire.

Dentition very characteristic with pseudolateral and pseudocardinal teeth (Text-fig. 8*a–d*). On the left valve, a strong pseudocardinal chevron-shaped tooth with an anterior point is flanked by two sockets, the posterior of which, in the concavity of the chevron, is very deep; the two pseudolateral teeth are long and lamellar; one of them begins on the fore part of the hinge plate, the other is thinner, and starts behind the beak; neither is microcrenulated. On the right valve, the plate shows the replicate elements with a pseudocardinal chevron-shaped tooth situated very anteriorly, less developed, and preceding a deep V-shaped socket; the ventral pseudolateral tooth is situated on the edge of the plate; the dorsal pseudolateral tooth is shorter.

This description is of material from the Iberian Peninsula and the Armorican Massif. It agrees too with material from Bohemia designated *Redonia bohemica* by Barrande (1881). Replicas of this species, from the National Museum of Prague sent to us by Dr J. Kříž, show only the posterior part of the lateral teeth. However, in latex moulds of specimens from his own collection (Šárka Formation, Llanvirnian), as he wrote (pers. comm., 1985), 'none of them shows crenulations of the lateral teeth'. We can see, also, that the plate under the umbo, illustrated by Pojeta (1978, pl. 4, fig. 2) is identical to that of *R. deshayesi*. Other specimens from Wosek (Bohemia) given by Barrande to de Verneuil and now housed in Lyon (Text-fig. 9*a–c*), are sometimes designated *R. deshayesi* and at other times *R. bohemica*. When they cited the occurrence of *R. deshayesi* in Spain, de Verneuil and Barrande (1856, p. 687) added 'cette espèce se trouve aussi dans les schistes du même âge à Vitré, à Gahard, à Monteneuf en Bretagne et en Bohême'. This material exhibits some variation; the Bohemian specimens are smaller than the Breton and Spanish ones, and the internal mould of the anterior adductor is less pointed, although we have intermediates from elsewhere. The dentition, however, is identical with the dorsally very concave small pyramid of the chevron-shaped socket, visible on the internal mould of the right valve (Text-figs 8*b* and 9*a*). Thus, we consider all these geographical varieties as conspecific.

R. michelae Babin, 1982, from the Arenigian of the Montagne Noire (South of France) is a distinct species. It is smaller and has a different shape of the anterior adductor; in internal moulds there is a lamellar pillar with a ridged top, perpendicular to the cardinal line; similarly, on the mould, there is a narrow and elongate adductor pit and a large septum, very different from *R. deshayesi*. Nevertheless juveniles of *R. deshayesi* (CC-I 2 212/OR, CC-I 2 213/OR) show a similar morphology (Text-fig. 10) suggesting an evolutionary hypermorphosis for the genus *Redonia*.



TEXT-FIG. 10. *Redonia deshayesi* Rouault, 1851. Umbonal region of the latex replica of a juvenile specimen (CC-I 2 212/OR); the aspect of the muscle scar and of the myophoric plate is very similar to *R. michelae* from Arenig (see Babin *et al.* 1982, pl. 10, fig. 4).

Genus DULCINEAIA n. gen.

Derivation of name. Dulcinea, a figure from *Don Quijote de la Mancha.*

Type species. Dulcineaia manchegana n. sp. here designated.
Diagnosis. Redoniidae with lamellar and microcrenulated pseudocardinals; elongate pseudolaterals variably microcrenulated.

Dulcineaia manchegana n. sp.

Plate 7, figs 1–8

?1912 *Redonia* Rouault, Douvillé, p. 441, figs 14 and 15.
1978 *Redonia deshayesiana* Rouault, Pojeta, pl. 4, fig. 5.
1984*b* *Redonia deshayesi* Rouault, forma *β*, Gutiérrez-Marco *et al.*, p. 302.

Holotype. Internal mould of a right valve showing the dentition, CC-I 2 140/OR.

Type locality and horizon. SE of Calzada de Calatrava (Ciudad Real), 70 m S of the km 47,500 of C-410 highway, just at the dam base of the Fresneda reservoir, right bank. Middle part of the Guindo Shales, late Lower Llandeilo (top of the Tournemini Biozone).

Derivation of name. After La Mancha region, Don Quixote's country, near to which important Ordovician fossil localities are located.

Paratypes. CC-I 2 074/OR-2 077/OR, 2 084/OR, 2 088/OR, 2 090/OR, 2 094/OR, 2 097/OR, 2 110/OR, 2 126/OR, 2 139/OR; PZ-III 2 102/OR-2 107/OR, 2 193-2195/OR; RA-I 2 109/OR, 2 111/OR, 2 119/OR, 2 126/OR; RE-VII 2 108/OR.

Diagnosis. As for genus.

Description and discussion. Shell equivalve, with an oval outline and strongly inequilateral with the umbo at the anterior. This morphology is similar to *R. deshayesi* and the two species are not distinguishable by their shapes. Posterior adductor muscle scar oval, large, placed under the end of the hinge plate, and weakly impressed. A small pedal retractor lies above it. Two other accessory scars are sometimes observed in the umbonal region of the shell; one is situated in front of the adductor, at one third of the distance to the beak, the other, smaller one is at half of that distance (Pl. 7, fig. 4). The anterior adductor scar is deeply impressed and corresponds, on the internal moulds, to a strong pillar, as in *R. deshayesi.* However, the shape of the pillar is a little different; the point, generally more obtuse, is rather more oriented towards the anterodorsal angle of the valve and its upper face is less strongly concave than in *R. deshayesi.* This morphology, combined with the differences of the pseudocardinal tooth, distinguish the two species in the internal moulds (the most common material) when observed by their anterior side and even if the microcrenulations of the teeth cannot

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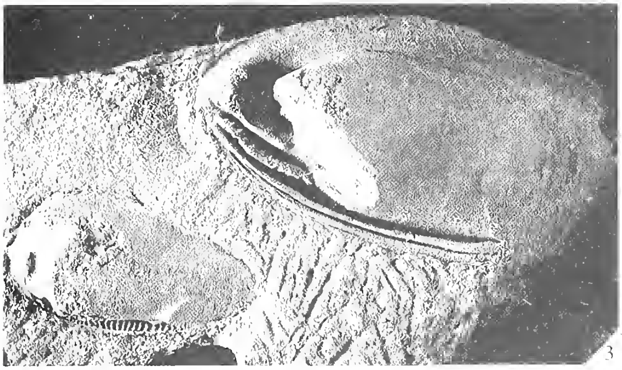
EXPLANATION OF PLATE 7

Figs 1–8. *Dulcineaia manchegana* n. gen., n.sp. 1, 3–8, Calzada de Calatrava (Ciudad Real), middle part of the Guindo Shales, late Lower Llandeilo. 1, holotype, internal mould of a right valve (CC-I 2 140/OR), ×4; 3, paratype, internal mould of a right valve accompanied by a right valve of *Myoplusia* (CC-I 076/OR), ×3; 4, dorsal view of internal mould of a right valve showing the microcrenulations on a tooth and accessory muscle scars (CC-I 2 110/OR), ×8; 5, latex replica of the same specimen, ×9; 6, paratype, latex replica of a right valve showing the dentition; 7, internal mould of a left valve (CC-I 2 097/OR). ×2.8; latex replica of the same specimen. ×4. 2, Pozuelos de Calatrava (Ciudad Real), Valdemosillo Shales, Upper Llandeilo. Detail of the microcrenulated anterior tooth on the left valve of a relatively young specimen; latex replica (PZ-III 2 105/OR), ×8.

PLATE 7


1


2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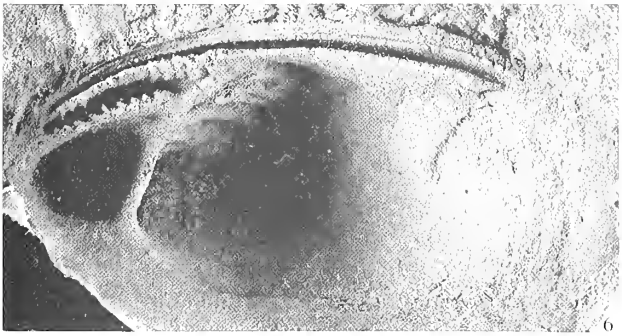
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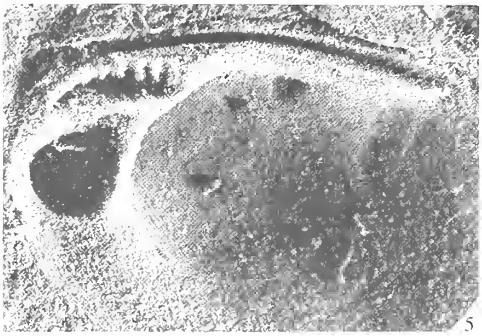
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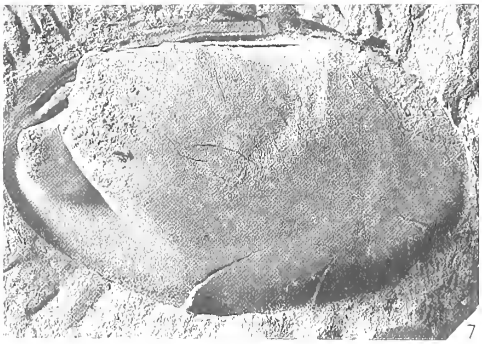
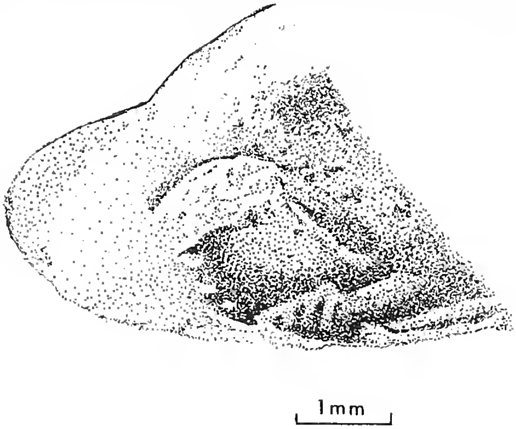

7

BABIN and GUTIÉRREZ-MARCO, *Dulcineaia manchegana* n.gen., n.sp.



TEXT-FIG. 11. *Dulcineaia manchegana* n.g. n.sp. Anterior dorsal region of the internal mould of a right valve (CC-I 2 076/OR) showing the microcrenulations on the tooth and three minute scars between the adductor pit and this tooth.

be seen. Some specimens show a series of minute scars (2–5) on the basal part of the anterior adductor (Text-fig. 11).

The dentition of *D. manchegana* is distinctive. The left valve shows a short lamellar tooth, situated under the umbo in a ventral position and directly bordering the deep adductor scar. The faces of this tooth are microcrenulated during early ontogeny (Pl. 7, fig. 2); it ends posteriorly near the myophoric buttress. A long, pseudolateral tooth, begins at the fore part of the shell, at about the same place as the ventral tooth; it is generally microcrenulated in its anterior region and, sometimes for up to 3/4 of its length (for example the paratype CC-I 2 097/OR).

The systematic position of *Dulcineaia* is not clear. We place it tentatively in the Redoniidae but the microcrenulations of the teeth pose a problem. Another genus with crenulated teeth, *Noradonta* Pojeta and Gilbert-Tomlinson, 1977, has been included in the Lyrodesmatidae, and Babin (1982) has referred to it a species from the Arenig, *N. redoniaeformis* (Thoral), which has a similar morphology (the type-species, *N. shergoldi*, also has a deeply impressed anterior adductor muscle). However, the species of *Noradonta* have several anterior teeth below the beak which more or less radiate from it; moreover the posterior elongate teeth are strongly crenulated. On the other hand, *Dulcineaia* has only one or two teeth beneath the umbo which are parallel to the dorsal margin of the shell; and like the pseudolaterals, they are slightly microcrenulated for part of their length or even entirely smooth. We suggest this species is allied to *Redonia* but it is clear that the differences between these genera are becoming less conspicuous with the new discoveries.

Finally, it is interesting to note that the stratigraphic distribution of *D. manchegana* is more restricted than that of *R. deshayesi*. The latter is known from the Llanvirn (Armorican Massif, Bohemia, Portugal, Spain, Morocco) and it continues in the Lower Llandeilo even when *D. manchegana* appears (the two species are present simultaneously in locality CC-1). Afterwards *D. manchegana* seems to remain alone in Upper Llandeilo levels together with the trilobites *Placoparia borni*. In this way, *D. manchegana* could be an index fossil but its geographic extension may have been restricted. In the literature, Douvillé (1912, p. 441) has figured two valves of *Redonia*, the dentition of which suggests that they belong to *D. manchegana*. This material came from the Ordovician of Brix (Normandy) and is in the collections of the Ecole des Mines (Paris), at present in Lyon. We have found in these collections two right valves from the same locality (and probably from the Moitiers d'Allonne Formation) and they are exactly determined *R. deshayesi* by the shape of the teeth without microcrenulations (Text-fig. 9*e*). So, the observation of Douvillé remains enigmatic. On the other hand, we have found in de Verneuil's collections, in Lyon, some poor but interesting specimens from Vitré (Brittany); the morphology of the anterior adductor and the visible part of the dentition show that they do not belong to *R. deshayesi*; they may in fact be *D. manchegana*.

SOME THOUGHTS ON EARLY ORDOVICIAN BIVALVE PHYLOGENY

'The strength of any phylogenetic hypothesis must be found in its corroboration by disparate data sets' (Laws and Fastovsky 1987). Among these data sets, morphology and stratigraphic superposition are both incomplete but their 'value and significance in phylogeny reconstruction are unquestionable'. With these remarks in mind, what can we attempt with respect to Ordovician bivalve phylogeny? The present material from the Middle Ordovician is interesting because in the Llanvirn a marked explosion of diversity of bivalve faunas occurs.

After the first known minute bivalves (Fordillidae) from the Lower Cambrian, the pelecypods remain very poorly known from the Middle and Upper Cambrian and during the Tremadoc, with only five or six species worldwide (Pojeta 1985: Pojeta and Runnegar 1985) and the age of some of these, like *Afghanosdesma* (Desparmet *et al.* 1971), is uncertain. The faunas from the Arenig are also geographically restricted despite some radiation. During the Llanvirn, the diversity of the faunas increases, but they are dominated by palaeotaxodontids and actinodontids. The phyletic relations of these two groups remain obscure. In the opinion of Douvillé (1912), Babin (1966), Morris and Fortey (1976), and Morris (1978), the actinodont type was probably the more primitive. Pojeta (1978) expresses doubt about this after the description by Allen and Sanders (1973) of the curious living deep-sea protobranch *Praelametila* and he concludes 'which group gave rise to the other is not clear'. Since the recent study on *Pojetaia* and its earlier appearance (Pojeta 1985), Pojeta and Runnegar (1985) admit that the heteroconchs might be descended from the paleotaxodontids; the latter are considered as occurring earlier, but this needs confirmation, in particular from the fauna described by Harrington (1938) from Argentina. It seems that 'during the Lower Ordovician, nuculoids are not so well represented as the Cycloconchacea' (Morris 1978). In contrast, during the Middle Ordovician, paleotaxodontids appear more diversified. Praenuculidae with an elongate anterior end become abundant. *Cardiolaria*, with resorption during ontogeny of the umbonal teeth, might 'indicate a very early stage in the migration of the external ligament onto the hinge plate' (Bradshaw 1970). *Ekaterodonta hesperica* is a Llanvirn species of this genus originally described from the Arenig of the Montagne Noire (Babin 1982) and which is related to another Llanvirnian genus from Spitzbergen, *Tironucula* Morris and Fortey, 1976. The potential phyletic interest of these forms is to show the possible evolution of a pseudolateral tooth 'by extending one arm of the V (of a chevron tooth) and suppressing the other', as described by Allen and Hannah (1986) with regard to the Recent and conservative Lametilidae and Siliculidae. The arrangement of the pedal muscles of the Ordovician paleotaxodontids is also primitive (cf. *Myoplusia*) and is later modified in the Upper Palaeozoic protobranchs (Driscoll 1964).

However, in the actinodontids, the diverse arrangements of the teeth justify the taxonomic discrimination of several genera, even though some of them are monospecific, and there is a rapid diversification. The relationships between them remain imprecise because of the durations of these stages (about 20 My for Llanvirn and Llandeilo together, after Odin 1985) and the incomplete biostratigraphical record. In addition, we are not able, on the present data, to decide on ancestral and derived characteristics in the arrangement and structures of the teeth. Thus, we cannot suggest precise phyletic relationships other than to underline some particularities of the species described above.

The dentition of *Ananterodonta*, known from a single specimen, resembles that of the living solemyoid *Nucinella* of which Allen and Sanders (1969) said 'it should be considered as a rather specialized member of the Actinodonta'. This remarkable fossil, may give us an indication of the pteroconch Cyrtodontidae in the trend of reduction of the anterior part of the posterior pseudolaterals.

Another problem concerns the relationships between actinodontids with and without microcrenulations on the teeth. A review of the presence of microcrenulations in diverse Palaeozoic bivalve groups, to compare with the ontogeny of living pelecypods, has been made by Babin and Le Pennec (1982). Microcrenulations are known from the Upper Tremadoc and the Arenig in *Babinka* and lyrodesmatids like *Tromelinodonta* and *Noradonta*. The discovery of *Dulcineaia* poses the problem of the relationships of this genus with *Redonia*, and others. Formerly, it was considered that 'it is highly likely that *Redonia* developed from a form with a dental plate similar to that of *Actinodonta*. The fusion of the teeth in both forms follows a similar pattern but has been more extreme in *Redonia*' (Bradshaw 1970), following research on *Actinodonta naranjoana*

(= *Glyptarca ? lusitanica*). It appears that *Redonia* was derived from a primitive actinodontid, but it is not a descendant of *Glyptarca?* which appeared later. Morris and Fortey (1976) granted particular phyletic importance to the microcrenulations, suggesting 'that the origin of the posterior hinge teeth in the Nuculoida ... is by the breakup of originally radiating "actinodont" teeth by enlargement of their transverse ridges'. Nevertheless, microcrenulations appeared independently several times; early (Upper Tremadoc-Lower Arenig) in *Babinka* and lyrodesmatids, and later (Upper Llanvirn-Llandeilo) in cycloconchids with the single genus *Glyptarca ? lusitanica*. There, only the posterior pseudolaterals are microcrenulated; this phenomenon appears early during ontogeny but the microcrenulations are less developed than forms like *Noradonta*. By contrast, *Glyptarca?* seems to be a cycloconchid acquiring crenulations rather than a lyrodesmatid reducing them. We have shown that a specimen from the Upper Llandeilo (Text-fig. 6*f*) has crenulations on its anterior tooth. As it is not apparently a senile avatar, was it a teratological feature or a prophetic one without continuation because of the disappearance of the genus?

Still more curious and obscure are the relationships between *Redonia* and *Dulcineaia*. The former is known, in its typical morphology (*Redonia michelae*), as early as the Lower Arenig from the Montagne Noire. It remained without notable changes during the Llanvirn and the Lower Llandeilo (*R. deshayesi*); suddenly, during the Llandeilo, the genus *Dulcineaia* appears with a very similar morphology to *Redonia* but with different cardinal teeth. Are they only homeomorphs or are they really related? We have preferred the latter alternative and placed *Dulcineaia* among Redoniidae. Is it an atavic reappearance of an ancestral form and how did it occur? Is it a true innovation, i.e. a case of divergence? This phenotypic novelty certainly did not appear as a response to new constraints, since *Redonia* and *Dulcineaia* lived together, in a similar habitat and we do not see structural modifications either of the whole shell or of the hinge plate. Unfortunately, we are not in a position to compare the ontogenies of the two genera. The mode of bivalve preservation as internal moulds is not suitable for the examination of very minute specimens. Finally, we have a young specimen (CC-I 2 100/bis/OR; right valve) showing a socket followed by a bud, but we cannot assign it to either of the genera because they coexist in the locality; the juveniles are possibly indistinguishable.

We should bear in mind, as with the microcrenulations, that the trend towards production of crenulated teeth is common among actinodontids and their descendants. Later, a similar feature occurs in the Devonian genus *Tanaodon* Kirk, considered by Pojeta and Runnegar (1985) to be 'a late surviving actinodontoid'. Heidecker (1959) has figured strong microcrenulations in *Neoactinodonta*, which is considered a junior synonym of *Tanaodon* and so, in the Treatise, *Tanaodon* is defined as 'with or without cross striations' on the teeth. This however is probably a character without important taxonomic significance and therefore we can place *Glyptarca?* in the Cycloconchidae and *Dulcineaia* in the Redoniidae. Still more surprising is the development of crenulations on the teeth among paleotaxodontids, like some *Nuculites* during the Devonian (Babin 1966). In such cases, the teeth beneath the umbo also show stronger crenulations than the posterior ones. The function of these microcrenulations is not clear, because, according to Allen and Hannah (1986), 'the nuculoid tooth in multiple array forms an incredibly strong hinge and in some species it is impossible to open the shell wide without shearing the teeth'. *Nuculites* has a myophoric buttress, also a character of *Dulcineaia* and *Noradonta*, but with a different orientation in relation to the hinge margin. In the actinodontids the microcrenulations restrict movement forwards and backwards and in the palaeotaxodontids they restrict dorsoventral sliding. There do not seem to be any general constraints governing the evolution of microcrenulations in bivalves.

THE PALAEOECOLOGY AND PALAEOGEOGRAPHICAL SIGNIFICANCE OF THE MIDDLE ORDOVICIAN BIVALVE FAUNAS

Since a subsequent paper will include detailed palaeoecological analysis of these formations, our treatment here is brief. There is, in this area, a relative stability in composition of the benthic assemblages, with bivalves, brachiopods, trilobites, echinoderms and ostracodes co-occurring for some 10 to 15 My; thus the trophic structure evidently remained nearly the same for a long time. In these assemblages the bivalves are mostly shallow-burrowing, with deposit feeders the dominant trophic group and with small body sizes. Like Frey (1987*a*), we tabulate here the mode of life of the observed genera (Table 1).

TABLE 1.

Genera	Mode of life
Palaeotaxodonta	
Praenucula	infaunal deposit feeder
Ekaterodonta	infaunal deposit feeder
Myoplusia	infaunal deposit feeder
Cardiolaria	infaunal deposit feeder
Heteroconchia	
Babinka	shallow infaunal filter feeder
Coxiconcha	shallow infaunal filter feeder
Glyptarca?	shallow infaunal filter feeder
Redonia	shallow infaunal filter feeder
Ananterodonta	shallow infaunal filter feeder
Pteriomorphia	
Cyrtodontula	endobyssate filter feeder
Isofilibranchia	
'*Modiolopsis*'	endobyssate filter feeder

After the first minute bivalves of the Cambrian, a progressive increase in size characterizes the Ordovician diversification. There is some variation according to environment. During the Arenig, for example, bivalves are large but are very scarce in the Armorican Sandstone, while they are numerous and small in the muds and sandy muds of the Montagne Noire. In the muddy Middle Ordovician facies of the southern Perigondwanan platform, they are generally small, with some exceptions like *Cadomia* and *Coxiconcha* or, occasionally, with individual gigantism (we have one specimen some 60 mm long). During the Late Ordovician, it seems that there is a further increase in size. Most of the studied faunas came from mudstones and siltstones. All these burrowing forms lived in soft sediments, mainly muds or muddy silts. Several were very shallow burrowers. Two specimens of *Glyptarca?* (FO 2 135/OR and CC-I 2 208/OR) and one of *Redonia* (CC-I 2 211/OR), for example, show a bryozoan incrustation (Pl. 6, fig. 1) suggesting that this part of the shell projected above the sediment-water interface; this attitude is similar to that figured by Frey (1987*a*, fig. 7) for *Cyrtodontula sterlingensis* which is a homeomorph of *Glyptarca?* Two specimens of *Praenucula sharpei* show small pits on the ventral part (Pl. 1, figs 5 and 6); identical pits in a pallial position occur in a specimen of the same species from the Armorican Massif (FSL 550 091).

Comparing localities, at La Vibora (the fossils were collected by P. Rossi about 1974), the facies is a fine shallow-water sandstone; the coquina is composed mostly of bivalves; among 177 fossils, there are 167 bivalves (94% of the fauna), 2 rostroconchs (*Ribeiria*), and 8 brachiopods (*Heterorthina*). The bivalves are *Praenucula costae* (43·7%), *Cardiolaria beirensis* (27·5%), *Glyptarca ? lusitanica* (21·6%), and small undetermined paleotaxodontids (7·2%). The age is probably Upper Llandeilo, and this may explain the absence of *Redonia*, but other forms known in these levels, such as *Dulcineaia manchegana* and *Myoplusia bilunata*, also seem to be lacking. Among our localities, a deeper water bivalve assemblage is apparently provided by site CR II, a black muddy facies with an undisturbed assemblage of numerous small specimens of *Redonia deshayesi* and other species such as *Ekaterodonta hesperica*, *Goniophora* sp., and cf. *Ctenodonta escosurae*. We consider this locality as corresponding to the offshore shelf. Therefore, we agree with

Morris (1978) that as early as the Lower and Middle Ordovician, some bivalves inhabited this part of the shelf in western Europe, while in North America (Frey 1987*a*, *b*) the first intrusions into offshore shelf environments by pelecypods occurred only during the Late Ordovician. It is worth noting that among the fauna of this locality the genus *Ekaterodonta* occurs, described from the Arenig of the Montagne Noire (Babin, 1982) and which appeared here as a conservative form in the deeper water habitats.

Finally, we can attempt to consider the spatio-temporal distribution of these faunas, their relationships with the ancestral Arenig stocks, and we can attempt to evaluate migrations and their causes. Before plate tectonic reconstructions, Spjeldnaes (1961) correlated Ordovician faunal provinces with climatic zones. Several palaeogeographic reconstructions have been produced during the last fifteen years. Bouyx (1988) has compared these different reconstructions; some of them, like that of Smith (1981) appear inconsistent with the data on facies and faunas. Most of them agree roughly with that of Text-figure 12 as regards the southern hemisphere during the Early Ordovician.

The distribution of bivalve faunas has rarely been considered, though since they are benthic they are worth including. A comprehensive worldwide comparison, however, still requires many investigations. Numerous regions are poorly documented and new studies can bring important fresh data (see for Australia, Pojeta and Gilbert-Tomlinson 1977, or for Bolivia, Babin and Branisa 1987).

The present area belongs to the *Selenopeltis* trilobite province of Whittington and Hughes (1972) and, more interesting for facies control, our faunas belong to the characteristic assemblages of fossils termed the *Neseuretus* community type by Fortey and Owens (1978), a community considered to have been shallow-water and inshore in clastic facies. A cool environment is inferred from the latitudinal position of the *Neseuretus* community. In this reconstruction, the postulated Proto-Tethys of Whittington and Hughes (1972) is abandoned; high palaeolatitudes from France and Iberia were confirmed recently by palaeomagnetic data (Burrett 1983). Nevertheless, Hallam (1984) reminds us that eustatic events 'were in general more significant than temperature' in controlling faunal provinciality. With the revival of interest in global changes of sea level (Vail *et al.* 1977), Fortey (1984) has examined the biological implications of these changes during the Ordovician; he gave a sea level curve for Tremadoc to Caradoc with an important regressive-transgressive event at the Arenig-Llanvirn boundary and another one during the Llandeilo; this postulated global eustatic curve is shown more precisely in Fortey and Cocks (1986).

The relationships of the southern Gondwanan shelf to other parts of Europe have also recently been discussed. Whittington (1963) postulated a marine barrier between Gondwana and Baltica (see also Babin *et al.* 1980), but its dimensions were probably not important (Bouyx 1988); this was recently named Tornquist's sea by Cocks and Fortey (1988). The detailed palaeogeography of the Gondwana platform itself during the Lower and Middle Ordovician is not clearly established Several areas appear distinctive, and Cocks and Fortey (1988) suggested 'a deeper water tongue between Armorica and Iberia running from the region of Ancenis, Brittany to the Montagne Noire in Southern France'. The Ossa Morena Zone in southern Spain is also anomalous. The Spanish faunas tell us that extension of the range of bivalves was caused by the widespread Llanvirnian transgression. But the Ordovician radiation for example (Sepkoski 1979) took place in the pelecypods of the Perigondwanan area during the Arenig rather than 'in the transition from the Lower to Middle Paleozoic' period of increase for marine benthic faunas (Bambach 1977). We do not know where the diversification of the bivalve communities took place in the Perigondwanan ring. During the Arenig, pelecypods are cited at low latitudes (Argentina, Australia) and at higher latitudes (Montagne Noire, Armorican Massif, Wales). The poor correlations between these areas do not permit determination of the thermal preferences of the primitive bivalve populations. On the southern Gondwanan shelf in the Montagne Noire, corresponding to the 'deeper water tongue' on the platform, pelecypods are known as early as the Late Tremadoc (*Babinka*) and then diversified during the Lower Arenig (*Babinka*, *Redonia*, *Synek*, *Thoralia*, *Noradonta*, *Coxiconcha*, *Ekaterodonta*); they inhabited fine sediments and probably cool waters. This area could have been the place of origin of several genera. During the Upper Arenig, some pelecypods of larger size colonized

TEXT-FIG. 12. Distribution of some bivalve genera during Arenig (Montagne Noire) and Llanvirn-Llandeilo (other countries) on the Perigondwanan platform. Palaeogeographic reconstruction after Gutiérrez-Marco and Rábano (1987); land areas are shaded. See also Cocks and Fortey (1988) for biofacies distribution around Gondwana.

shallow-water sands like those of the Armorican Sandstone, with actinodontids, lyrodesmatids (*Tromelinodonta*), and scarce palaeotaxodontids (*Praenucula oehlerti*). The rapid expansion of the Llanvirn is not uniform and, during the whole Middle Ordovician, the reasons for particular distributions and migrations remain obscure. Among the palaeotaxodontids, which often constitute the dominant element, the genus *Praenucula* is common in the Ibero-Armorican province as well as Morocco, Bohemia or on the marginal edge of the shelf (e.g. Ardenne) but the species are not determined with certainty and it is difficult to follow the possible migrations. The case of *Ekaterodonta* is peculiar. This genus, known in the Arenig from the Montagne Noire, appears like a relict in some deeper facies during the Llanvirn from the Hesperian Massif but it is present at the same time in Bolivia at a lower latitude, and the first described Tironuculidae, *Tironucula*, is a contemporaneous form from the Laurentian platform. During the Llandeilo, *Myoplusia bilunata* existed in Brittany and Spain (and perhaps in the Ardenne?); and persisted into the Caradoc in the Armorican Massif and Bohemia. But another common Ibero-Armorican species, *Cardiolaria beirensis*, is unknown elsewhere. Still more curious, *Tancrediopsis ezquerrae*, a common form in Portugal and Brittany, remains to be found in the Spanish area.

If we compare the palaeotaxodontids from other areas of the world, we can see a sudden diversification during the Llanvirn in varied facies from lower latitudes (North America, Baltica, Australia, South America). In these regions there are representatives of *Ctenodonta* and *Deceptrix* but also there are often numerous genera unknown in the Ibero-Armorican region, like *Similodonta?* in Norway (Soot-Ryen and Soot-Ryen 1960) or the various genera described from Australia, such as *Eritropis* and *Johnmartinia*, which are frequently found in sandstones (Pojeta and Gilbert-Tomlinson 1977).

The isofilibranchs and pteriomorphids are scarce in the Ibero-Armorican area; but they are more frequent and diversified in Baltica (Soot-Ryen and Soot-Ryen 1960) in the more calcareous facies and warmer waters.

The actinodontids and their problematic allied genera, *Babinka* and *Coxiconcha*, are also interesting in their spatio-temporal distributions. *Babinka prima* appears early in the Upper Tremadoc in the Montagne Noire and it remains until the Upper Arenig in this region where post-Arenig rocks are unknown. During the Llanvirn, the same species occurs in Bohemia and in the Hesperian Massif, but it remains unknown among similar communities and environments in Portugal and in the Armorican Massif. On the other hand, *B. oehlandica* was described by Soot-Ryen (1969) from Baltica around the Arenig-Llanvirn boundary. Thus, from the Montagne Noire, *Babinka* migrated to some sites on the southern Gondwanan shelf without recognizable specific variation during a time interval of about 20 My and it crossed Tornquist's sea to reach the Baltica shelf, giving rise to another species. *Coxiconcha* is also known from the Montagne Noire as early as the Lower Arenig and remained there during the whole stage. During the Llanvirn and Llandeilo, the genus was abundant, with a larger species *C. britannica*, in the muddy sea floors of the Ibero-Armorican area and it migrated along the Gondwanan coast giving another species in Bolivia. However, it remains unknown from Bohemia.

Among the Cycloconchidae, *Glyptarca* ? is a genus with a widespread distribution on the southern Gondwanan shelf. Originally described from Portugal, it is common from the Middle Ordovician in the whole Ibero-Armorican province, usually in muds, but sometimes adapted to sandy sediments. *Glyptarca* is cited from Saudi Arabia (Fortey and Morris 1982) and may occur in Morocco (Babin unpublished) but is unknown from Bohemia (Born 1918). Finally, the Redoniidae present other differences. The first known *Redonia*, *R. michelae*, is known from the Montagne Noire, as early as the Lower Arenig. Like the other bivalves from these environments, relatively deep on the platform, this species is a small one. In the Armorican Sandstone, from the Upper Arenig, the poorly known *R. boblayei* (Barrois 1891) is larger. During the Llanvirn, *Redonia deshayesi* is an important element of the benthic Ibero-Armorican communities. It is also present in Bohemia in similar environments and in Morocco in sandy facies. The genus was cited as *R. anglica* in Shropshire by Salter (1866). *Redonia* appears to have been eurytopic with regard to grain-size but was probably a stenotherm, preferring cold water. We can thus explain its presence in the deeper zones of the platform (Montagne Noire during the Arenig; locality CR II in the Hesperian Massif and occurrence in the Ossa Morena Zone during the Llanvirn) as in the higher latitudes (Morocco). Around Gondwanaland *Redonia* is unknown from South America or Australia, where it was erroneously cited by Warris (1967) (after Pojeta and Gilbert-Tomlinson 1977). The new genus *Dulcineaia* is known only from the Llandeilo of the Hesperian Massif.

In conclusion, this study of Spanish bivalve faunas underlines the necessity for further new investigations. Bivalve distribution is apparently complex, with some endemics. To confirm this, more data are needed from the Ibero-Armorican area, the Bohemia faunas require revision, and the Moroccan ones need to be studied. As Boucot (1985) has stated 'the pelecypods are a group deserving a great deal more taxonomic attention and collecting before one can be certain of such conclusions'.

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SPONGIOPHYTON FROM THE LATE LOWER DEVONIAN OF NEW BRUNSWICK AND QUEBEC, CANADA

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ABSTRACT. Compressed cuticles of the dorsiventral, presumed parenchymatous land plant *Spongiophyton* are described from several late Lower Devonian (Emsian) localities in northern New Brunswick and Gaspé, Quebec. They are assigned to *Spongiophyton minutissimum* Kräusel. Thalli branch dichotomously several times in more than one plane and also produce short vertical branches. No reproductive structures are present. The cuticle is thicker dorsally, often being up to 250 μm thick as opposed to 30–60 μm for the ventral cuticle. Small circular to elliptical pores occur on the dorsal surface or along thallus margins. The many specimens obtained provide considerable information on variation in vegetative morphology and suggest a growth habit similar to some extant thallose liverworts. This new information expands the concept of *S. minutissimum* and supports the genus as a taxon quite distinct from *Nematothallus*, *Prototaxites*, or other plants with a putative filamentous organization. Absence of reproductive structures precludes improved understanding of *Spongiophyton's* relationship to algae or vascular plants; the presence of a resistant cuticle argues against these plants representing algae. They may instead represent a transitional grade between algae and higher plants. The new specimens also demonstrate that these cuticles are susceptible to some differential breakdown as a result of oxidation or heat. Degradation features include superficial cracks or pockmarks, a spongy appearance, or a pseudocellular pattern. It is suggested that possibly some features of other enigmatic Devonian plants (e.g. *Orestovia*, *Rhytidophyton*, etc.) may have resulted from degradation of their very thick cuticles.

IN addition to the many genera of vascular plants that are known to occur in the Lower Devonian of New Brunswick and Gaspé (for a summary see Gensel 1982), a variety of non-vascular plant types also are present. These may represent several genera and most probably several different lineages of non-vascular plants, many of which still require detailed study. This paper describes one very abundant form, obtained from several outcrops of Early Devonian rocks in New Brunswick and Gaspé, Quebec, referable to *Spongiophyton minutissimum* Kräusel.

These fossils were first collected by Sir J. W. Dawson and briefly described in his introductory comments appended to Penhallow's publication on *Prototaxites* of 1889. In those comments, Dawson (p. 34) noted 'In the sandstones of Gaspé basin there occur laminae of a resinous substance resembling amber ...' which often were associated with carbonaceous films. He concluded that these entities represented a secretion of the bark of some tree, suggesting somewhat indirectly that the source may have been *Prototaxites*.

Our investigations show that these fossils are not resinous secretions but rather are cuticles of thalloid organization referable to *Spongiophyton*, first described from the Middle Devonian of Brazil by Kräusel (1954). Kräusel established the family Spongiophytaceae to include *Spongiophyton*; this family subsequently was expanded to include up to 6 genera (listed in Table 1). Despite the diverse array of thalloid organisms included in the Spongiophytaceae, definitive evidence on their more exact affinities does not exist. They have been regarded as enigmatic terrestrial thallophytes with no known modern counterparts, possibly related to an algal division. All possess one feature not yet found among algae, namely a resistant cuticle. Whether or not all of the genera included in this family are closely related to one another remains uncertain.

Sommer (1959) recorded the genus in several Lower Devonian localities in the Brazilian states of Parana, Boias, Piaui, and Maranhao and in western Bolivia. Kräusel and Venkatachala (1966)

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TABLE 1. The six genera attributed to the Spongiophytaceae, with number of species in each and their distribution.

Genera	No. of species	Geographic distribution
Spongiophyton Kräusel	4	Brazil, Ghana, Canada, Poland(?), Bolivia(?)
Aculeophyton Kräusel and Venkatachala	2	USSR (Siberia), Brazil
Orestovia Ergolskaya	5	USSR (Siberia, Voronezh and other regions), China
Orestovites Istchenko and Istchenko	1	USSR (Voronezh region)
Rhytidophyton Istchenko and Istchenko	2	USSR (Voronezh region)
Voronejiphyton Istchenko and Istchenko	1	USSR (Voronezh region)

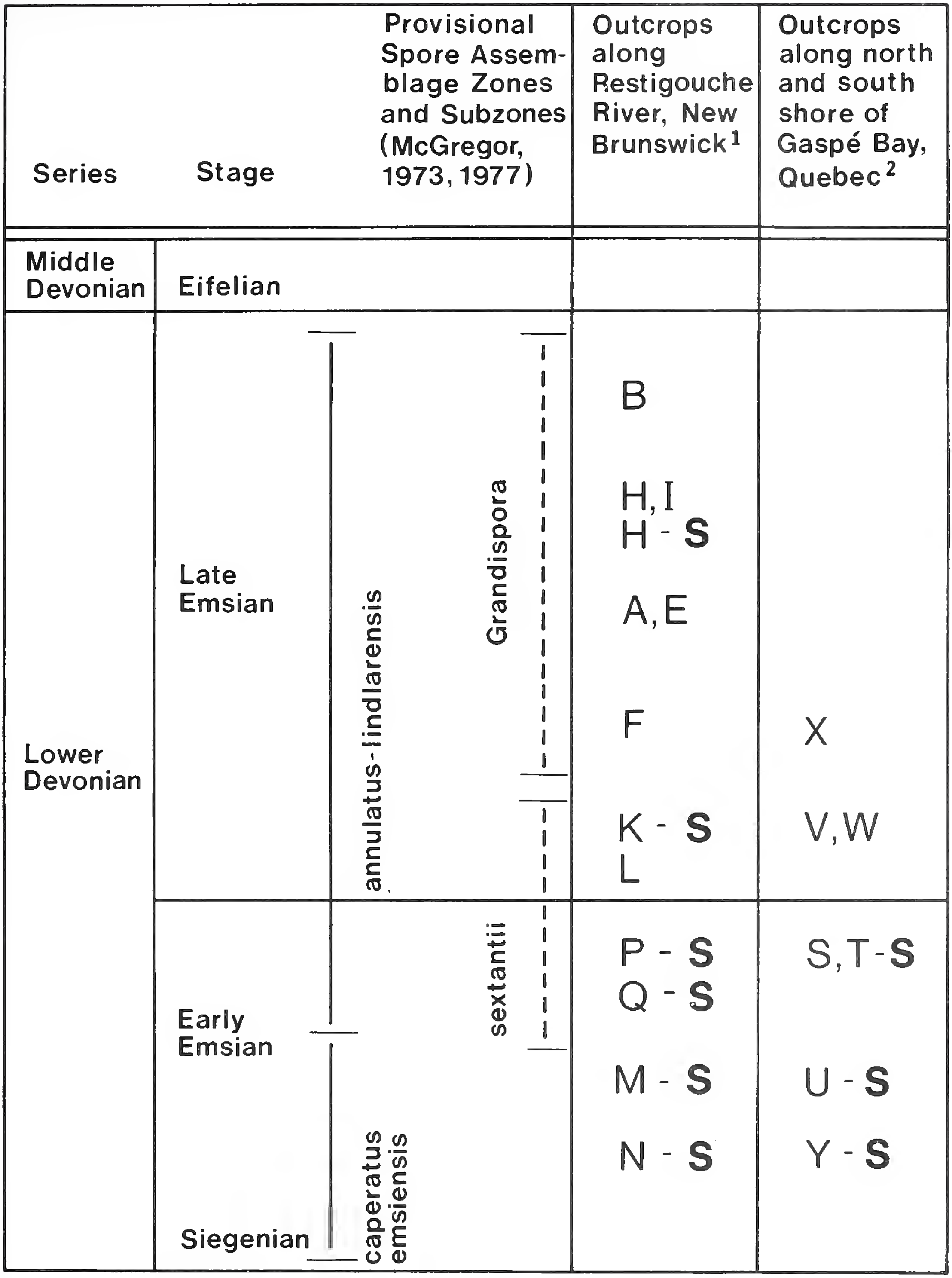
provided comparative data on several species of *Spongiophyton*, and suggested that *S. hirsutum* possibly belonged to their newly described genus *Aculeophyton*. They also described fossils as *Orestovia* from the Lower Devonian of Yunnan Province, China. They placed both *Aculeophyton* and *Orestovia* with *Spongiophyton* in the family Spongiophytaceae. Zdebska (1978) described fragments from a borehole in Poland as *Spongiophyton*, but Edwards (1982) suggested that these remains, particularly Zdebska's species 2, may have more features in common with cuticles attributed to the nematophytes than *Spongiophyton*. Chaloner *et al.* (1974) provided a detailed description of specimens from the Middle Devonian of Ghana which expands the circumscription of *Spongiophyton nanum* and documents the occurrence of remains similar to *S. lenticulare*. Boureau and Pons (1973) described remains from southern Bolivia which they assigned to *Spongiophyton lenticulare*, using these and associated plant remains to date the sediments as Early Devonian. Their identification may need reconsideration. Our report represents the first undoubted record of *Spongiophyton* from the Early Devonian.

Several similar types of plant, some of them included in the family Spongiophytaceae, were described by Istchenko and Istchenko (1981), thus demonstrating the existence of spongiophytes *sensu lato* in the Middle Devonian in parts of Russia. Some of these exhibit similar morphology to *Spongiophyton*, while others differ in cell construction. Again, their exact relationships are not clear.

The rather widely-ranging geographical distribution of the Spongiophytaceae *sensu lato*, including the fossils discussed here, is summarized in Table 1. The genus *Spongiophyton* occurs, without doubt, in South America and Africa at a high palaeolatitude (60° S or greater) in the Devonian. This report documents its presence in Laurussia-associated microcontinental plates at approximately 20–30° S. This might suggest that the plant exhibited a broad temperature tolerance, since the southern Gondwanan continents contain faunas indicating cool temperatures at that time (see Boucot 1985; Livermore *et al.* 1985; Scotese *et al.* 1985). Other genera attributed to the family Spongiophytaceae occur between 0° and 30° N palaeolatitude in Laurussia (?), Kazakhstania, Siberia, and China, where some form coals.

The abundance of *Spongiophyton* in the Canadian localities suggests that it was a common element of the vegetation, forming large populations in some areas. The large numbers of individual thalli obtained at some localities provide new information on the overall organization of the cuticularized thallus and on aspects of variation in this genus.

TEXT-FIG. 1. The occurrence of *Spongiophyton minutissimum* (heavy-type S) at various localities in New Brunswick and Quebec, showing their range in terms of the spore assemblage zones. Specific localities are discussed in the text.



Series	Stage	Provisional Spore Assemblage Zones and Subzones (McGregor, 1973, 1977)	Outcrops along Restigouche River, New Brunswick[1]	Outcrops along north and south shore of Gaspé Bay, Quebec[2]
Middle Devonian	Eifelian			
Lower Devonian	Late Emsian	annulatus-lindlarensis Grandispora	B	
			H, I H - **S**	
			A, E	
			F	X
			K - **S** L	V, W
	Early Emsian	sextantii	P - **S** Q - **S**	S, T-**S**
			M - **S**	U - **S**
	Siegenian	caperatus emsiensis	N - **S**	Y - **S**

([1] Outcrops designated A-N.)

([2] Outcrops designated S-Y.)

TEXT-FIG. 1. For legend see opposite.

LOCALITY AND GEOLOGY

The major localities yielding *Spongiophyton* are listed below and in Text-figure 1; these include some of Dawson's localities as well as other outcrops in New Brunswick and Gaspé, all of late Lower Devonian (Emsian) age.

1. Atholville, New Brunswick: Route 17 roadcut into Atholville (Locality P, Text-fig. 1) and outcrop along Beauvista Drive (Locality Q, Text-fig. 1). Specimens occur scattered on bedding surfaces of channel fills at the former and as stacks of individuals in grey bands of poorly-bedded sandy claystone at the latter.

2. Localities H, K, M, and N (Gensel and Andrews 1984; Text-fig. 1) along the Restigouche River, near Dalhousie Junction, New Brunswick, from which several vascular plants have been described (Gensel 1982). The thalli are sporadic and usually are intermixed with the more abundant vascular plant remains.

3. Cross Point, Quebec: at the Bordeaux Quarry and just to the north along Route 132. These rocks were included in the Gaspé Sandstone Group (McGerrigle 1950; Alcock 1935) and may fall within the LaGarde Formation of Dineley and Williams (1968). The Bordeaux Quarry, one of Dawson's collecting sites, consists of a sequence of red-brown sandstones alternating with conglomerate bands. The thalli occur in the sandstone along with slender ribbed axis (?*Psilophyton*) and *Prototaxites* 'logs'. These same sediments are exposed along a new roadcut on Route 132, where bedding surfaces show alternating conglomerate and sandstone layers, with the latter being a thin 'wash' of pebbles. Thalli densely cover the bedding surfaces of the sandy layers; a specimen of *Prototaxites* about 5 m long and 0·8 m wide and numerous smaller ones also were found in or immediately adjacent to these layers.

4. At several horizons of the Battery Point Formation near Cap-aux-Os, Gaspé and along the Laurencelle road which leads from Cap-aux-Os to Cap-des-Rosiers Est, Gaspé Peninsula, Quebec (localities S, T, U, Y of Gensel and Andrews 1984; Text-fig. 1). Thalli are rare to fairly abundant and appear to have been transported.

5. South shore of Gaspé Bay at several localities. (See McGregor 1977 for stratigraphic correlations.)

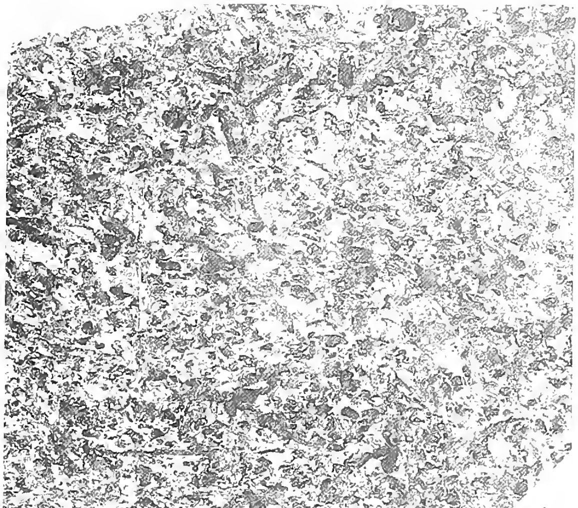
TAPHONOMY, MATERIAL AND METHODS

Considerable variation in mode of burial exists among thalli obtained from these outcrops. The majority are spread along bedding planes of fluvial, often channel-deposited sediments, with no preferred orientation (Pl. 1, figs 1 and 5), suggesting they were transported moderate distances prior to deposition. At locality Q, thalli occur in stacks several entities deep and are so tightly held together that it is difficult to determine if they represent one plant or several (Pl. 1, figs 2–4). Thick coverage of some bedding surfaces by many such stacks suggest that these thalli were growing in considerable abundance in some areas and buried rapidly near (or at?) their site of growth. We tend to discount the possibility that the stacks of thalli resulted entirely from the way in which they grew because they are not all orientated the same way up within a stack.

The thalloid plants are preserved as compressed cuticles which occasionally show impressions of internal cells, thus mostly demonstrating general morphology. We use the term *cuticle* to refer to the inert outer covering of these fossils. It is resistant to oxidative maceration and shows a pattern of cell outlines on the inner surface, features found in the cuticle of higher plants. Its chemical composition is unknown, but its morphology compares closely with the lipid-derived cuticle known to occur only in embryophytes (higher plants). Although some algae apparently possess a thin, protein-rich outer covering that withstands some acid hydrolysis (Hanic and Cragie 1969), these have not been shown to be resistant to coalification during fossilization.

EXPLANATION OF PLATE 1

Figs 1–7. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. 1–5, various ways the thalli occur in the sediment; 1, specimen from Route 132, Quebec locality with numerous scattered thalli on the bedding plane; this specimen was etched in HF, GSC 93004, ×0·8. 2, surface view of mass of thalli from a poorly bedded siltstone, Atholville locality, New Brunswick, GSC 93003, ×1·2. 3, lateral view of mass of stacked thalli, Atholville locality, New Brunswick, GSC 93005, ×1·4. 4, mass of stacked thalli from Atholville; N.B. locality, isolated by maceration in HF, GSC 93008, ×3. 5, numerous thalli after etching a single bedding plane, locality N, New Brunswick, GSC 93006, ×1·2. 6, SEM of thallus isolated by maceration, distal region to left; basalmost divisions produce upper and lower lobes (a), next 1–3 divisions produce side-by-side ones (b); note constrictions in lobes, pores (some indicated by arrows); roughness and cracks probably produced by deterioration under SEM vacuum, ×10. 7, thallus fragment with four dichotomies mostly in same plane, some with apices preserved, poral surface up, lying on etched surface of sediment, GSC 93011, ×4.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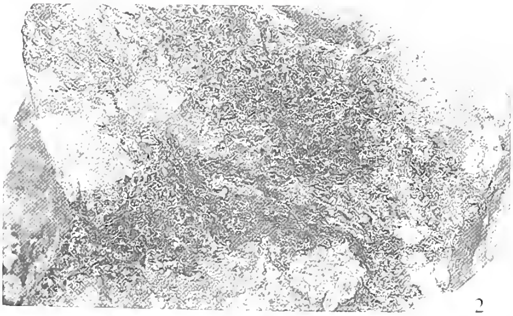
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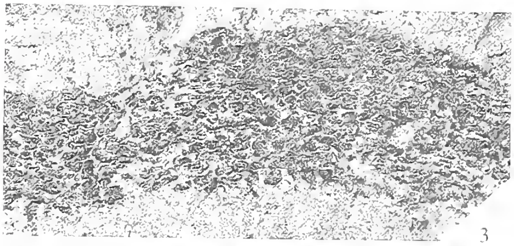
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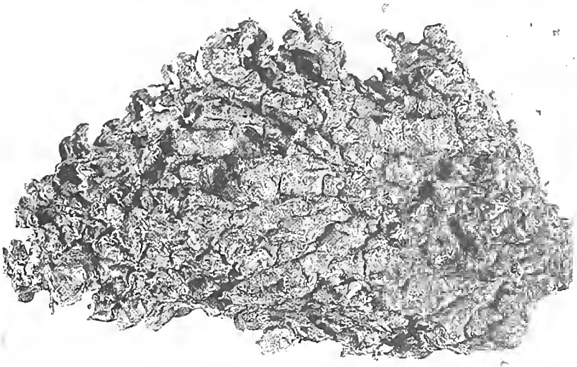
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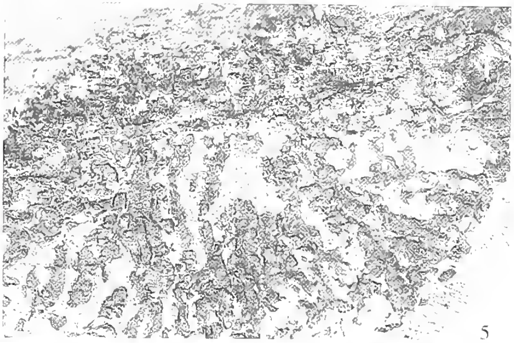
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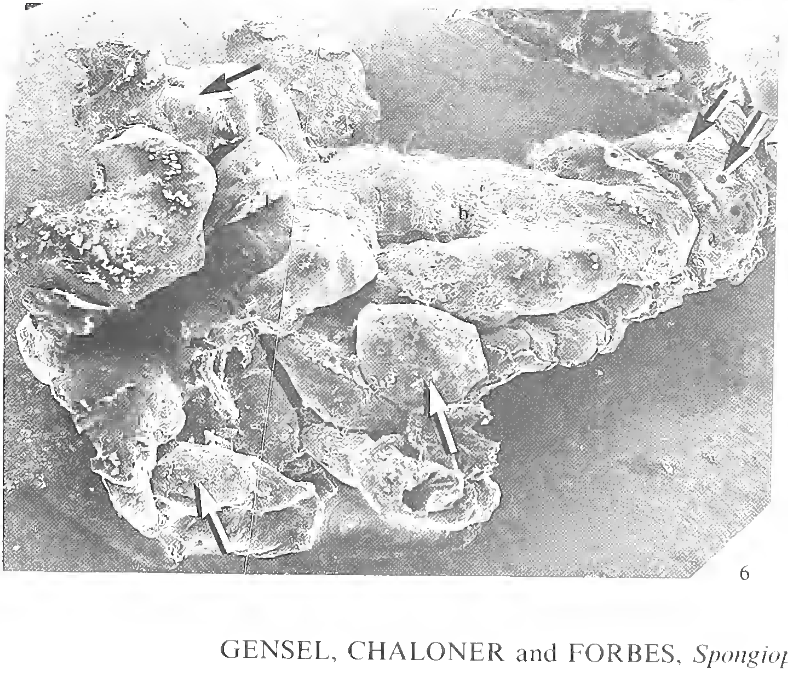

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GENSEL, CHALONER and FORBES, *Spongiophyton*

The cuticles range from a shiny to dull black or brown colour to ones which are naturally weathered to a red-brown colour. Some lighter coloured portions, especially distal tips, appear waxy. A single specimen may exhibit some portions that are red-brown and others, black; possibly it was specimens of this kind which caught Dawson's eye. Thallus surfaces range from smooth to finely pockmarked to rough in texture; the latter may have been partially corroded during diagenesis. At the Rte. 132, Quebec locality, the sandstone matrix apparently has imprinted outlines of grains on the thalli, causing a distinctive deeply pockmarked surface pattern.

Individual thalli, or regions of a given thallus, vary in the extent to which the cuticle is eroded. Many splits and cracks are present, and more may be induced during SEM treatment. Features we interpret as resulting from erosion include differences in pore outline, the frequent absence of the thinner, here designated lower, part of the thallus, and the depressions located at branch tips.

Bulk maceration of specimens in HF provided best results in elucidating thallus morphology. Thalli cleared only after long oxidation in Schulze's solution. Individual fragments reacted slightly differently to oxidation, suggesting that alteration of the original substance prior to or during fossilization was quite variable. Selected specimens were cleared in Shulze's solution at timed intervals, being examined and photographed with a light microscope at 10, 30, and 60 minute intervals. At the end of 48 hours, no evident destruction of surface features, or changes in pore outline or size, were observed in well-preserved specimens. In poorly preserved thalli (partially oxidized, possibly more strongly compressed), pores became progressively more irregular in outline with prolonged maceration. Extensively cleared thalli may appear 'cellular' as a result of differential breakdown of the thick cuticle (Pl. 3, figs 5 and 6). Differential erosion, particularly of the inner cuticle surface, is evident in thin sections (Pl. 3, fig. 1). After long maceration the cuticles appear spongy in construction (Pl. 3, fig. 7). This probably was the basis for Kräusel's original suggestion of a spongy structure (Schwammstructur) of the thallus (see also Chaloner *et al.* 1974, p. 934).

To determine regularity of pore spacing, camera lucida drawings were made of specified areas of selected specimens. Using a customized software program called MEASUR (S. Case, pers. comm.) pore location was digitized, spacing calculated, and mean nearest neighbour determined. No regular pattern was evident.

Rock fragments containing numerous thalli and individual thalli isolated by maceration in HF were embedded in plastic, sectioned, and ground thin until transparent. Isolated thalli also were embedded in araldite or glycol methacrylate, sectioned with a microtome, and examined with LM and TEM for ultrastructural detail.

Both oxidized and unoxidized specimens were mounted on slides in CMC non-resinous mounting medium, or were glued to glass or cardboard slides with gum tragacanth. Isolated thalli were also mounted on stubs, coated with gold-palladium and examined with an ETEC SEM. Specimens were photographed using a Leitz Aristophot, a Wild Photomacroscope, or a Zeiss photomicroscope. Type and figured specimens are stored in the collections of the Geological Survey of Canada at Ottawa, Ontario and bear the numbers GSC no. 93003–93020.

SYSTEMATIC PALAEONTOLOGY

Family SPONGIOPHYTACEAE Kräusel, 1954

Genus SPONGIOPHYTON Kräusel, 1954

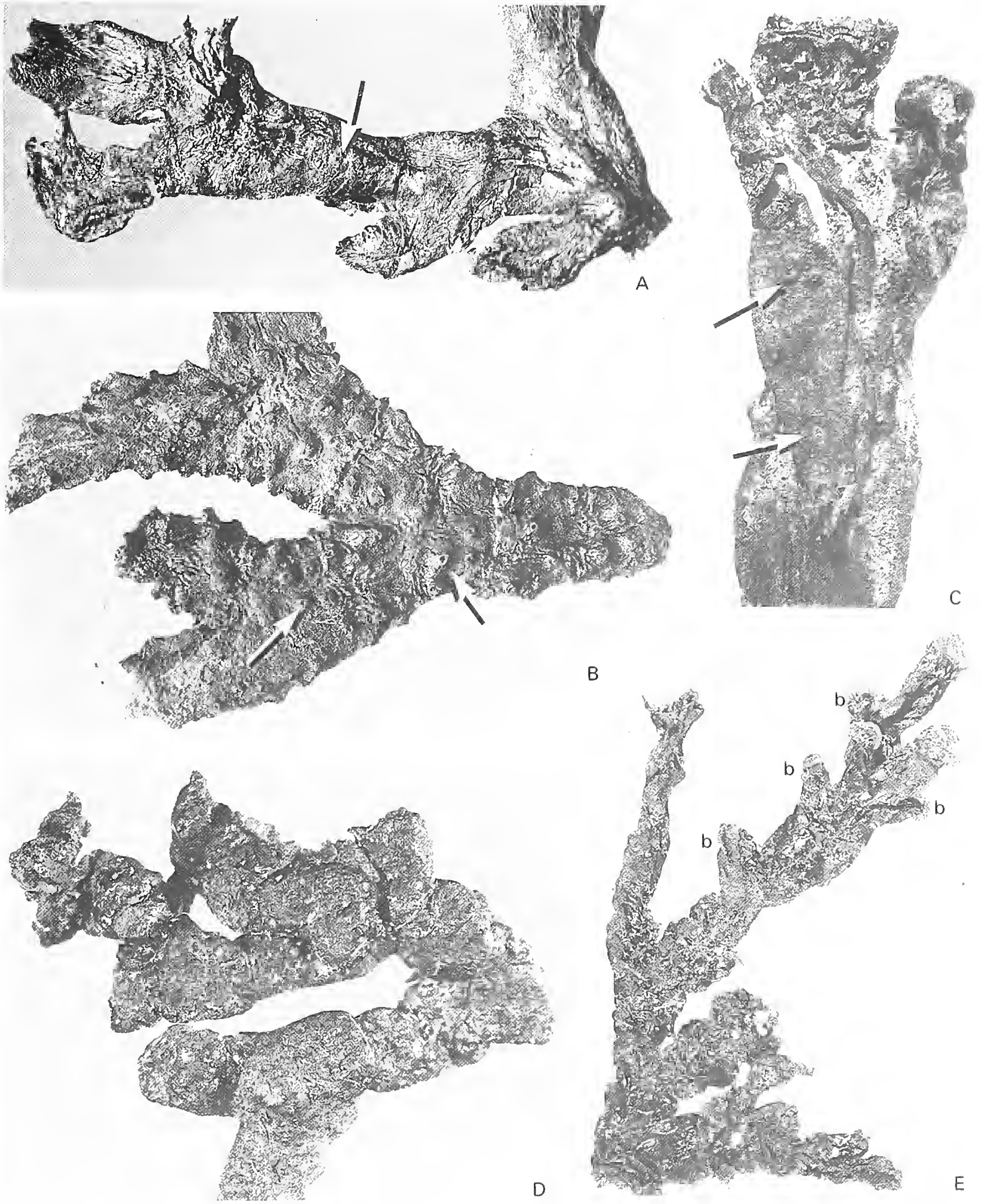
Type species. Spongiophyton lenticulare (Barbosa) Kräusel, 1954, p. 206, figs 5–7 of Barbosa, 1949; from the upper Punta Grossa beds, Parana, Brazil.

S. minutissimum Kräusel, 1954

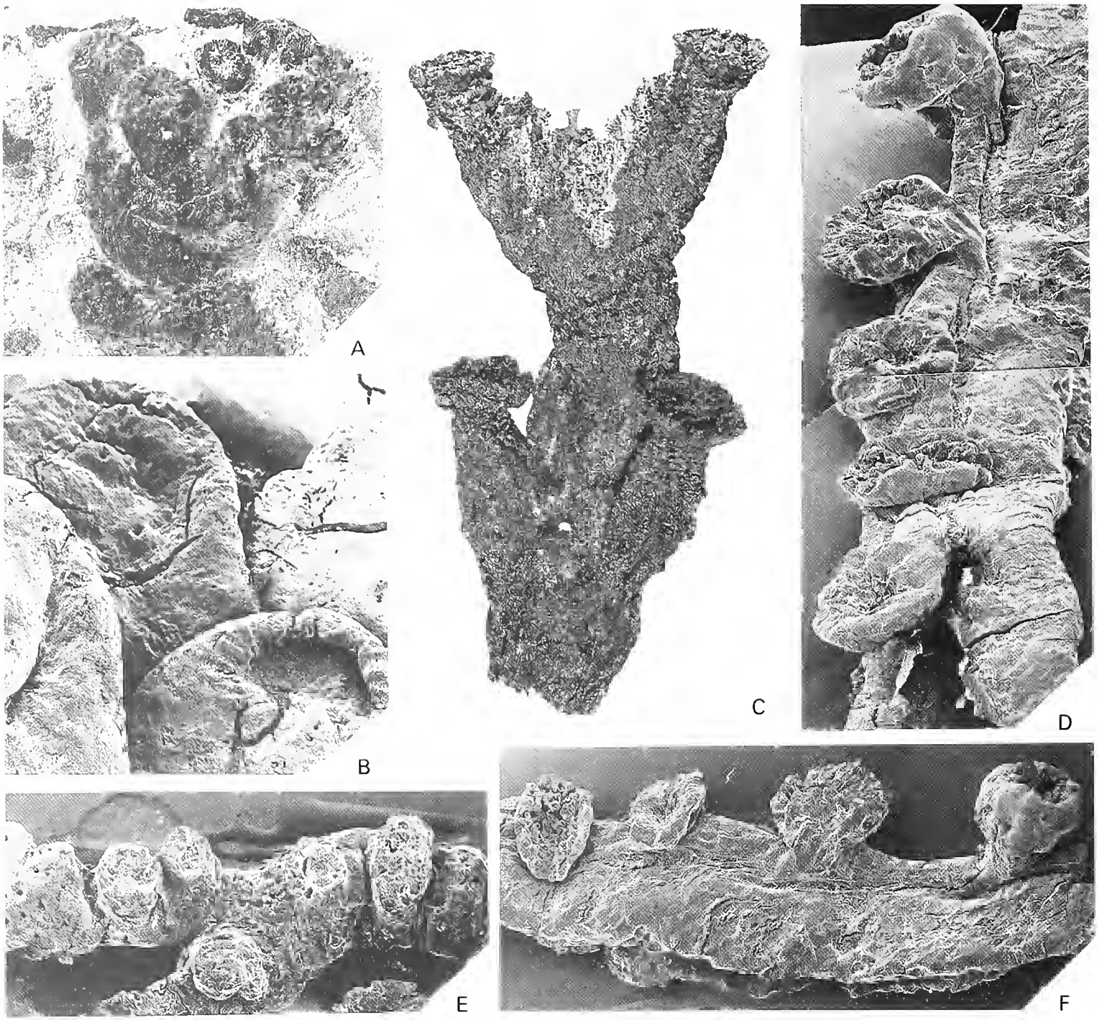
Plates 1–3; Text-figs 2–6

Type specimens. P. 264/9, Kräusel (1954), Pl. 28, figs 72 and 73.

Original diagnosis. Thallus klein, meist nur wenige mm messend, gabelig gelappt, mit stark verdickten Rädern. Innenbau wie bei *Sp. nanum*, die zahlreichen Löcher aber klein, nadelstichartig, ihre Durchmeser meist 60 bis 100, selten bis 150 μm, oft quer verbreitert, Oberflächenzellen wabig-vieleckig.

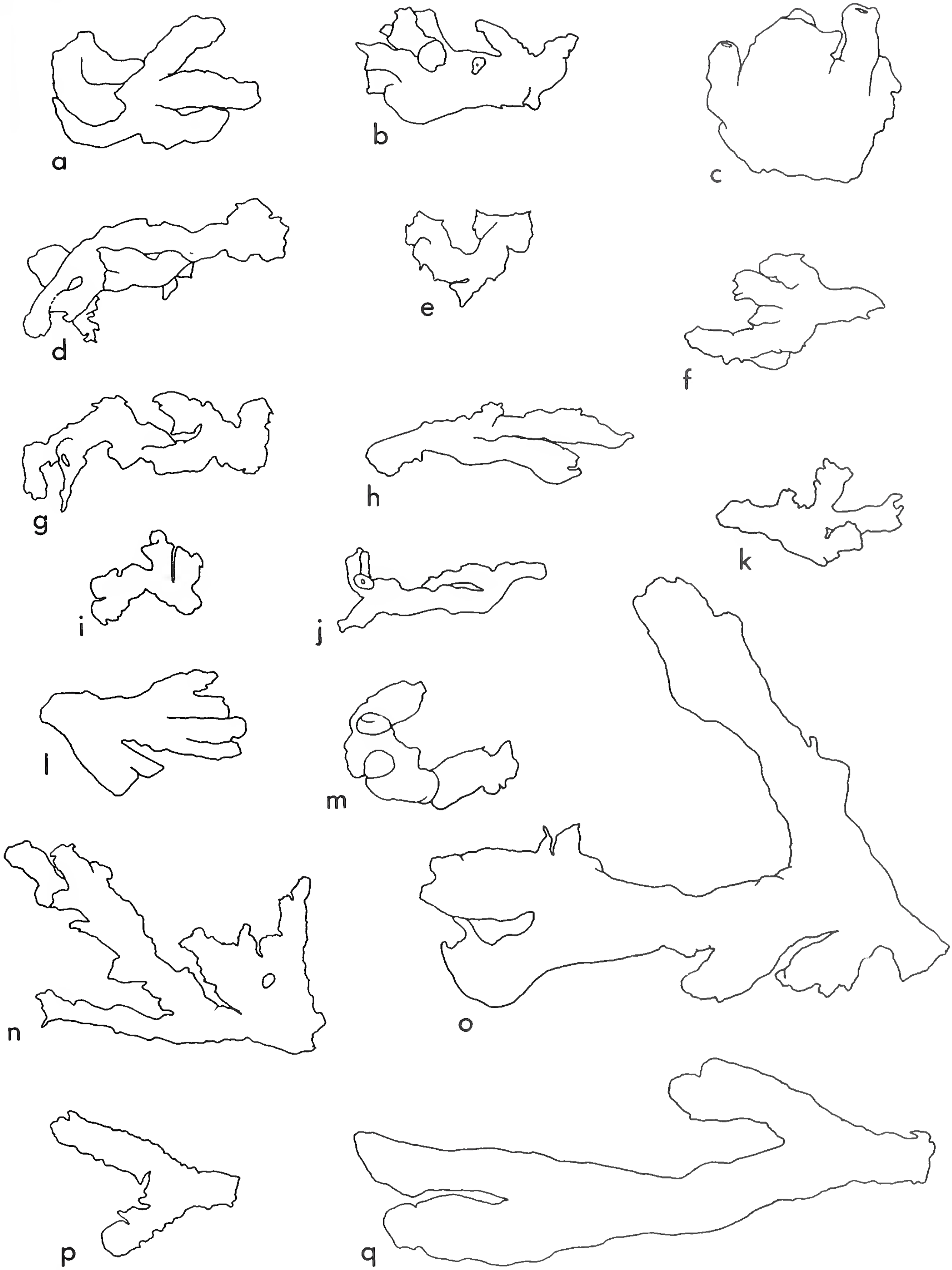


TEXT-FIG. 2. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. A, form 3 thallus, poral side up, with smooth to finely ridged surface and few pores (one at arrow); branching is mostly in one plane; wrinkling and constrictions near lobe apices are interpreted as a result of preservational factors, GSC 93012, × 7. B, form 2 thallus, poral surface up, with many pores (arrows), each pore located in raised area of surface producing bumpy appearance. GSC 93013, × 12. C, form 3 thallus fragment isolated by maceration, showing two dichotomies in two different planes, but with lobes parallel (arrows indicate pores), GSC 93010, × 14. D, form 1 thallus with numerous constrictions, dichotomies in same plane, numerous pores, GSC 93015, × 12. E, form 1 thallus bearing numerous short branches (b) as well as exhibiting major dichotomies, GSC 93016, × 9.



TEXT-FIG. 3. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. A, an isolated thallus with several lobe apices visible, after short HF etch; from sequence near *Sawdonia acanthotheca* locality (locality M), New Brunswick, GSC 93007, ×6. B, SEM of horizontal thallus lobes; note breakdown of apex to right and absence of spores or other cell masses in depression, ×46. C, LM of thallus with two pairs of lobes, intermediate between short vertical branches and 'normal' lobes, departing from poral surface; lobe apices collapsed, GSC 93017, ×10. D and F, SEM of thalli with short vertical branches departing from poral surface; apical depressions are probably a result of collapse of thinner cuticle in that area; D, ×15; F, ×11. E, SEM of thallus with very pronounced constrictions and possible short vertical branches near left, pores, ×12.

Emended diagnosis. Thallus cylindrical, originally circular or elliptical in cross section and at least 2 cm long. Width of thalli 0·2–5·5 mm. Thalli may exhibit constrictions along their length. Thalli branch dichotomously several times, with most lobes 3–10 mm long and with rounded apices. Short erect branches (1–2 mm long) occur on poral surface of some thalli. Pores extend through cuticle mostly on one surface, this being 2–4 times thicker than aporal surface (75–250 μm *vs* 30–60 μm), the thicker cuticle extending around the margins onto the edge of the aporal surface. Poral and aporal surfaces smooth, aporal surface often longitudinally folded. Inner surfaces of cuticle may



TEXT-FIG. 4*a–q*. Camera lucida drawings of various *Spongiophyton minutissimum* thalli, showing differences in extent and angle of branching, ×6.

retain rectangular cell outlines, 20–43 μm long and 9–12 μm wide, although often degraded and vermiform in appearance. Pores circular to oval, randomly spaced, $22{\cdot}5 \times 9$ μm to 99×90 μm in diameter, with vertical, fissured or (occasionally) bevelled edges.

Description. The plant fossils consist of the very thick cuticles of dorsiventral, apparently elliptical thalli which dichotomize at various intervals and on the surface of which pores occur (Pl. 1, figs 6 and 7; Text-figs 2–4). Thalli vary mainly in size, pore density and location, extent of branching, and surface features. Three categories (forms 1–3) of thalli are recognized: (1) the majority are smooth-surfaced, with a number of pores located on the upper surface, many branches, and 'constrictions' (Pl. 1, figs 6 and 7; Text-fig. 2D, E); (2) some are smooth-surfaced except that each pore occurs in a small projection resulting in an overall bumpy appearance (Text-fig. 2B); and (3) some thalli are smooth but longitudinally ridged, have very few pores located along lateral margins, and bear short vertical branches (Text-figs 2A, C and 3C). We presently regard this variability in surface topography, pore distribution, and branching type to be intra-specific, perhaps resulting from different parts of a given plant being represented, populational differences, and/or preservational differences. We thus refer all of the specimens to a single species.

The dorsiventral thalli are usually incompletely preserved, being up to 10 mm long and ranging from 0·3–2·5 mm wide (Pl. 1; Text-figs 2 and 3). The thick amorphous cuticle is smooth externally (Text-figs 2 and 3) and rough internally (Text-fig. 5C; D). One surface of the cuticle is thicker than the other (Pl. 3, figs 1 and 3); we interpret the thicker surface, on which pores and branches occur, to be the dorsal surface of a more or less flattened horizontal thallus. Pores may also occur near the margins on both upper and lower surfaces of some (especially form 3) thalli.

The thalli branch dichotomously at least six times at 0·2–3 mm intervals, being dense on some specimens and very sparse on others. Branching results in formation of lobes extending in the same plane as the original thallus (Pl. 1, fig. 7; Text-figs 2A, B and 3C) or in lobes lying one on top of the other but still with their long axes parallel (Pl. 1, fig. 6; Text-fig. 2C). These may curve upwards, downwards or laterally (in relation to the presumed horizontal position of the main thallus). It is not unusual to observe three to four levels of thallus lobes belonging to one specimen in the stacks of fossils preserved at the Atholville locality. Additionally, branching may result in one horizontal and one short vertical lobe at right angles to each other (Text-figs 2E and 3D, F).

Constrictions occur within the lobes of some thalli resulting in a sausage-string type of appearance (Pl. 1, fig. 6; Text-figs 2D, E and 3E. The region between some constrictions almost resembles very short upright branches.

The upright branches are 1–2 mm tall and occur singly or in 2 rows (Text-fig. 3D, F). While upright branches occur on all forms of thalli, they are most abundant on form 3, being located along a central ridge area. Most exhibit pores (Pl. 2, fig. 2). The branches are narrower towards their base and swell or flare distally (Text-fig. 3A, C, D, F). Some of these branches terminate in rounded apices, often with a slight depression (Pl. 2, fig. 1; Text-fig. 3A). A few exhibit small protrusions extending from the apex (Pl. 2, figs 3 and 4) while others have at their tips a deep cup-like depression which usually is irregular in outline (Pl. 2, fig. 2). The interior of the cup revealed no organization such as spores or vegetative propagules. Their structure suggests the depressions formed as a result of collapse and breakdown of cuticle at the branch apex. Horizontal branch tips exhibit similar depressions (Text-fig. 3B).

Circular to oval shaped pores occur on the presumed upper (and thicker) surface of the first two forms of thalli and along the margins of the third form of thallus (Pl. 1, fig. 6; Pl. 3, figs 5 and 6; Text-fig. 2B–D). They are variably spaced, from 3·5 μm to 350 μm apart. Average distance between pores on selected specimens are 30, 53, 75, 178, 222 μm. The pores range in size from 22·5 μm long by 9 μm wide to 99 μm long by 90 μm wide. SEM study shows the pore margin often to consist of indented fissures or rounded outlines (Pl. 2, figs 4 and 6; Text-fig. 5B). Only a few exhibit a bevelled edge (Pl. 2, fig. 5) as has been described in *Spongiophyton nanum* by Chaloner *et al.* (1974).

EXPLANATION OF PLATE 2

Figs 1–5. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. 1 and 2, SEM of apical region of vertical branches showing various degrees of collapse; 1, × 40; 2, × 31. 3 and 4, general view and detail of short vertical branches with protrusion at apex – also appearing somewhat degraded; note occurrence of pores on branches (arrows); 3, × 38; 4, × 120. 5, SEM of pore with bevelled edges, some evidence of internal surface of cuticle, × 1100. 6, SEM of pore with irregular margin, × 120.

PLATE 2


1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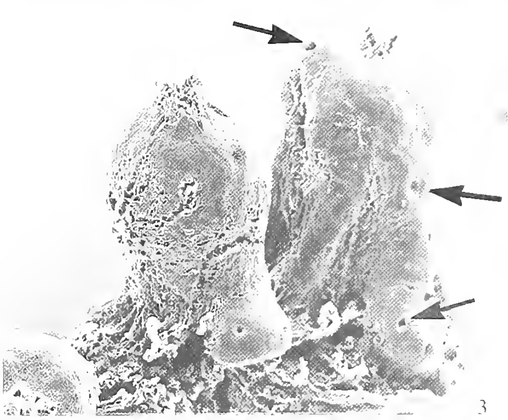
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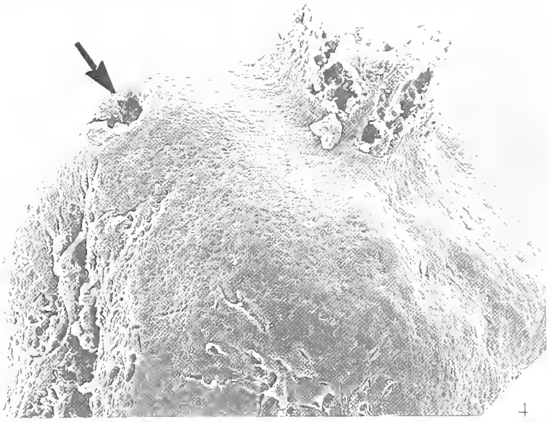
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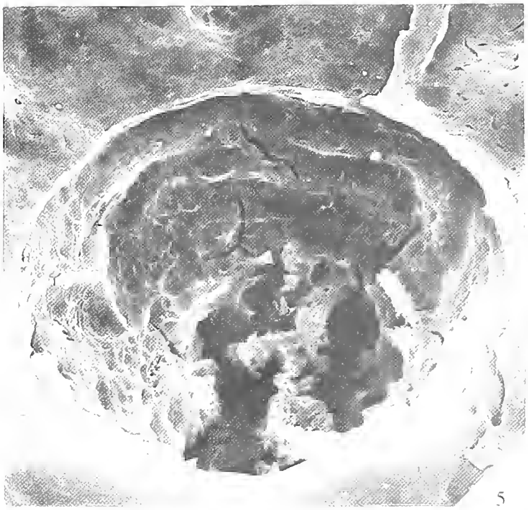
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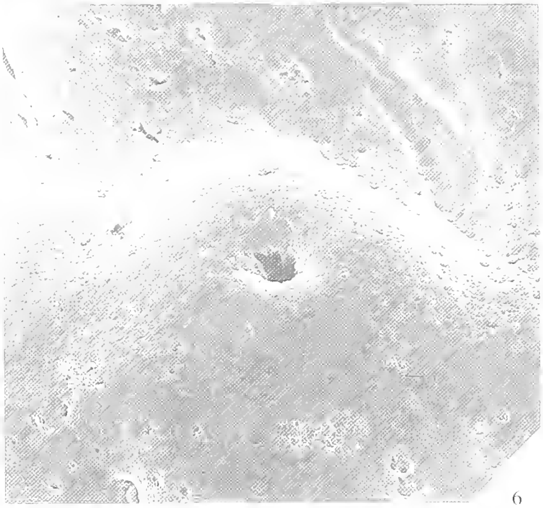
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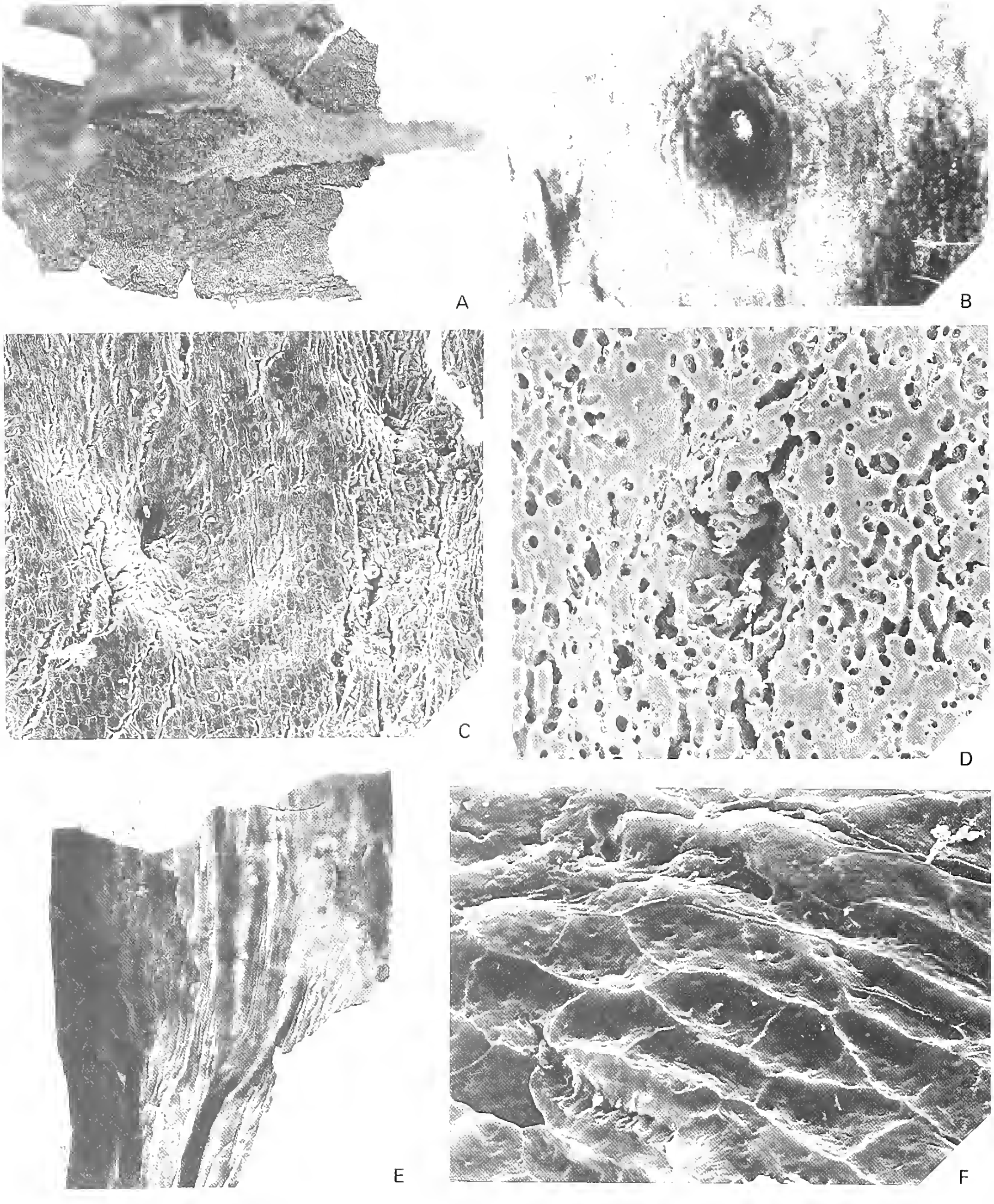
GENSEL, CHALONER and FORBES, *Spongiophyton*



TEXT-FIG. 5. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. A, interior contents of a thallus, GSC 93014, × 14. B, LM of pore on thallus cleared with Schulze's solution until nearly translucent; region around pore is darker than rest, GSC 93020, × 65. C, SEM of inner cuticle surface, poral side, showing outlines of rectangular cells; pore in centre, × 110. D, SEM of inner cuticle surface, poral surface, appearing vermiform, probably a result of degradation or borings; pore in centre, × 220. E, ventral surface of extensively cleared thallus with characteristic longitudinal folds, GSC 93018, × 31. F, SEM of inner cuticle surface showing rectangular cell outlines; this probably reflects type of cell construction immediately below the cuticle, × 550.

Thickness of the poral, presumed upper surface is 75–250 μm, and that of the aporal one is about 30–60 μm. However, the form 3 thalli exhibit poral and aporal surfaces of more equal thickness. The thinner lower thallus surface often is partly broken down or may be entirely absent (Text-fig. 5A). Intact lower surfaces have been observed mostly near the tips of some lobes and rarely on more completely preserved specimens. Where present, the lower surface exhibits longitudinal ridges and appears fragile and rather wrinkled except at the margins where it is transitional to the thicker, upper surface (Text-fig. 5E).

Inside the thallus occurs a thin granular layer of material which is usually light-brown in colour (Text-fig. 5A). We do not believe this is rock matrix (left after HF treatment) but is a remnant of the internal contents of the thalli.

SEM of a cut transverse section of the thallus cuticle end-on shows it to be amorphous (Pl. 3, fig. 3). Thin sections examined with LM and TEM show an absence of internal structure in the cuticle, except for minute structures perpendicular to the outer surface interpreted as borings or cracks (Pl. 3, figs 1, 2, 4). Particularly interesting is the absence on all but a few specimens of regular ridges or pegs corresponding to depressions between epidermal cells as usually occurs on vascular plant cuticles or in other species of *Spongiophyton*. However irregularities of the inner surface of the cuticle may represent the position of anticlinal walls in life (Pl. 3, fig. 1). Possibly many such ridges were lost or obscured through erosion of the inner cuticle surface.

Examination of the interior cuticle surface has revealed few with cellular patterns (Text-fig. 5C, F). More frequently they exhibit a vermiform pattern (Text-fig. 5D) which compares well with the 'borings' described by Chaloner *et al.* (1974) for *S. nanum* from Ghana. Cleared thalli may exhibit an apparent cell-like pattern (Pl. 3, figs 5 and 6), especially in photographs. Close examination suggests these result from cracks caused by differential breakdown of the cuticle after prolonged oxidation. We term this a **pseudocellular pattern** and regard it as different from the cell outlines preserved on some inner cuticle surfaces.

Elemental analysis of two different specimens show element ratios similar to the Ghana *Spongiophyton* specimens (Table 2).

TABLE 2. Elemental percentage composition of *Spongiophyton* from Canada and Ghana. The difference of the sum from 100 is probably accounted for by oxygen.

	N	C	H	S
S. minutissimum, Canada	1·18	74·88	8·08	0
S. minutissimum, Canada	1·03	69·01	7·55	0
S. nanum, Ghana	2·70	78·40	8·40	—

COMPARISONS AND DISCUSSION

The thalli are clearly referable to the genus *Spongiophyton* Kräusel as emended by Chaloner *et al.* (1974). Characters considered diagnostic of the genus by the latter authors, and exhibited by the Canadian material, are: a tubular thallus with cuticular covering, dichotomous or sub-dichotomous branching and rounded apices; cuticle with internal cellular reticulum and circular-fusiform pores largely confined to one surface of the thallus. The Canadian specimens are older and morphologically more diverse than other undoubted *Spongiophyton* specimens. The thalli branch much more frequently and in more than one plane, and also bear more short vertical branches than previously known. Our data also confirm the interpretation of Chaloner *et al.* (1974) that some features considered diagnostic by Kräusel (dark bodies on surface, the 'spongy' or hyphal pattern) are in fact the result of degradation, either during preservation or the clearing process, of the thick cuticles. A pseudocellular pattern may result from cuticular breakdown in the Canadian specimens. The constrictions common in the Canadian thalli probably are a result of preservational factors or may reflect environmental fluctuations.

Species of Spongiophyton

The Canadian specimens are most similar to Kräusel's species *S. minutissimum*, based on consideration of his few illustrations and brief description and on study of his figured specimens. Many extensively cleared thallus fragments from Canada are identical to *S. minutissimum* in exhibiting thickened margins, a character considered by Kräusel as distinctive for that species. Thallus appearance, cuticle thickness, and pore shape, size, and density of the Canadian material corresponds very closely to *S. minutissimum*. Two possible differences exist – maximum thallus width in the type material (up to 5 mm) exceeds that of the Canadian fossils and the dark bodies described by Kräusel for *S. minutissimum* are not found on the Canadian specimens.

The more extensive preservation and greater abundance of specimens from Canada provides some characters not available from the type material, limiting further comparison. In the absence of major characters separating them, and indeed with strong evidence supporting their identity, it seems reasonable to expand the concept of a known species rather than create a new one.

Differences between the Canadian specimens and other species of *Spongiophyton* include pore morphology and size, thallus size, and cuticle thickness. *S. nanum* and *S. lenticulare* are the best known species. The Canadian specimens differ from *S. nanum* in their smaller pores that mostly lack a bevelled margin. Branching is more profuse in the Canadian specimens than in *S. nanum* where only a few dichotomies or vertical branches have been recorded. Thallus diameter is half that of *S. nanum*. Cuticle thickness of the Canadian specimens (up to 250 μm) is much greater than that of *S. nanum* (60–80 μm) and both exceed the thickness of most vascular plant cuticles.

Similarly, the Canadian specimens differ from *S. lenticulare* in pore morphology, those of the latter species being elongate, slit-like structures with folded edges of cuticle extending to the outside, and their thicker cuticle. The internal cellular pattern of *S. lenticulare* consists of more elongate cells than occur in either *S. nanum* or the Canadian material.

Kräusel and Venkatachala (1966) placed *S. hirsutum* in *Aculeophyton*, because of its hairlike papillae. Kräusel's species *S. articulatum* is based on broken cuticle fragments which exhibit a very pronounced longitudinal striped pattern and transverse corrugations. These remains bear some resemblance to very over-macerated thalli from Canada, but are too poorly known for further comparison.

Notably absent in all of these species is any evidence of reproductive structures. Chaloner *et al.* (1974) suggested that the short vertical branches present on *S. nanum* thalli were perhaps sites of reproductive organs, but no conclusive evidence was obtained. Many short vertical branches of the Canadian specimens which exhibited depressions were examined for evidence of spores or other possible reproductive structures. Occasionally a mesh-work of material was present in the depressions, but more commonly only fissures were observed along the margins. Both types of structure are interpreted to have resulted from degradation of cuticle in apical regions.

Other identifications of thalli as *Spongiophyton* are less certain. Boureau and Pons (1973) assigned thalli from Bolivia to *S. lenticulare*. Pore shape agrees with that of Kräusel's *S. lenticulare* but some other features are problematical, recalling protuberances termed 'capsules' (see below) in *Orestovia* and other genera by Istchenko and Istchenko (1981). The Canadian specimens differ, not only in pore outline, but also in lacking dark round bodies and any evidence of internal 'hyphal ramifications' as described for the Bolivian specimens. The latter should be compared more closely

EXPLANATION OF PLATE 3

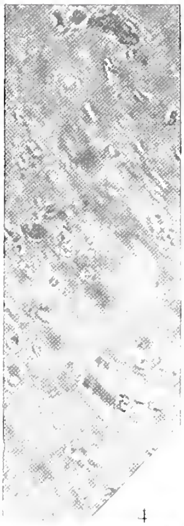
Figs 1–7. *Spongiophyton minutissimum* Kräusel from New Brunswick and Gaspé. 1, ground thin section of thallus in rock matrix, showing much thicker poral and thinner aporal surfaces; dark contents in middle may be remains of inner cells and may correspond to the lighter material seen in Text-fig. 5A, ×54. 2, TEM of cuticle showing absence of internal structure, except for possible borings, ×700. 3, SEM of transverse cut surface end-on showing differential thickness of poral and aporal surfaces and absence of structure other than borings, ×280. 4, LM of section of cuticle showing borings, ×300. 5–7, cleared thalli showing breakdown of cuticle producing a pseudocellular pattern; 5, cleared thallus fragment with thicker margins as illustrated by Kräusel as typical of this species; some evidence of pseudocellular pattern at arrow, shown enlarged in fig. 6, GSC 93019, ×31; 6, detail of pseudocellular pattern of specimen in fig. 5, can be emphasized by manipulating lighting of microscope; several pores visible, apparently 'ringed' by pseudocellular pattern, GSC 93019, ×65. 7, over-cleared cuticle with spongy appearance similar to several illustrated by Kräusel, ×39.

PLATE 3

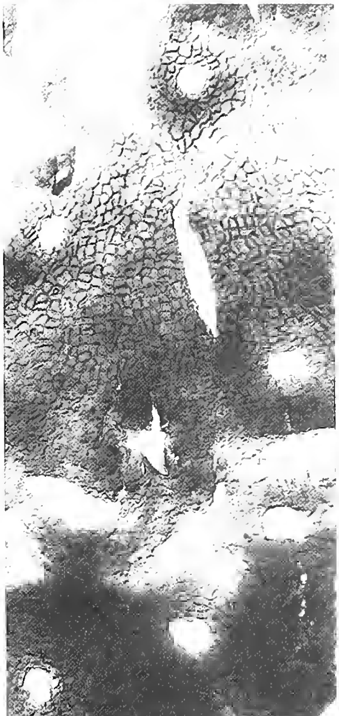

1


2


3


4


5


6


7

GENSEL, CHALONER and FORBES, *Spongiophyton*

to the several thalloid types described by Istchenko and Istchenko (1981) from the Voronezh anticline, USSR.

As noted earlier, the specimens described as *Spongiophyton* by Zdebska (1978) may in fact represent other taxa. Although Zdebska's species 1 bears a superficial resemblance to *Spongiophyton* thalli, no details of pore type or cellular construction are evident. Species 2 consists of fragmentary cuticles with isodiametric cell outlines and pores, suggesting a filamentous rather than parenchymatous organization. Neither type shows any indication of being part of a tubular thallus like *Spongiophyton*. Edwards (1982) suggested that these fragments resemble some cuticles of *Nematothallus*.

Other putative spongiophytes

Other genera are allied with *Spongiophyton* in the family Spongiophytaceae (Table 1) because they exhibit a thalloid construction with thick, resistant, sometimes flexible cuticles and lack definitive evidence of reproductive structures. Comparison of these taxa is hampered somewhat because interpretation of particular morphological structures varies, depending on the worker involved or the time of publication and corresponding knowledge of Devonian plant diversity. It also is extremely difficult to interpret structural detail on opaque cuticles of comparatively undifferentiated organisms from photographs and descriptions. The cuticles of these other taxa may also have been strongly affected by taphonomic factors and preparation techniques. Thus the family may not be as coherent as it appears.

The broad, ribbon-like cuticularized axes of *Orestovia* are generally similar to *Spongiophyton* but longer, wider, less frequently branched, radially symmetrical, and with a thinner cuticle. The outer surface is smooth or covered with some form of tiny emergence (depending on author). Circular pores with slightly raised margins, often bordered by several concentric layers of mostly isodiametric 'cells', occur randomly. Extraporal regions bear the outline of elongate-rectangular cells. The pores and associated structures are interpreted by some workers as stomata (Ergolskaya 1934, 1936; Krassilov 1981), and by others as reproductive structures (Kräusel and Venkatachala 1966, Istchenko and Istchenko 1981). Krassilov (1981) further reported the presence of conducting cells with thickened wall patterns in *Orestovia*, suggesting it may be a vascular plant. Our preparations of thalli, conforming to Ergolskaya's *O. petzii* from the Barzas coal, support some of his conclusions concerning stomata. Krassilov's specimen appears papillate (= *O. devonica* of Ergolskaya), whereas the specimens available to us are smooth. Obviously, further documentation is needed to resolve several attributes of the genus. Despite this, *Spongiophyton*, including the Canadian material, can be distinguished from *Orestovia* in gross thallus organization, symmetry, and details of pore construction.

The genus *Aculeophyton* was established by Kräusel and Venkatachala (1966) for cuticular fragments of thalli from western Siberia, originally placed by Ergolskaya (1934, 1936) in *Orestovia devonica*. The genus differs from *Orestovia* mainly in the presence of papillae, conical in *A. sibirica* and hair-like in *A. hirsutum*. Krassilov considered that other characters outweighed the presence of papillae and that *Aculeophyton* and *Orestovia* are synonymous.

Istchenko and Istchenko (1981) described several new genera and species of thalloid plants from the Lower Devonian of the Voronezh region, USSR, placing some in the Spongiophytaceae and some in a second family, the Bitelariaceae. Bitelarian cuticles reflect distinct 'cell' patterns interpreted by the Istchenkos as a meristoderm (without a cuticle) and by Johnson and Gensel (1989) as a cuticular epithelium. A number of other characters such as branching pattern and presence of vascular tissue in *Bitelaria*, further distinguish bitelarians from all thalli placed in the Spongiophytaceae, as summarized in Johnson (1989) and Johnson and Gensel (1987, 1989).

Istchenko and Istchenko (1981) assigned the Voronezh fossils to several genera (*Orestovia*, *Orestovites*, *Voronejiphyton*, *Rhytidophyton*, *Bitelaria* and *Donotela*) relating them to the algae. They interpreted the protruding round pores found on thalli of the first four genera as reproductive structures (termed capsules) reminiscent of conceptacles or nemathecia, as found in brown and red algae. When mature, each structure supposedly opened and released its contents, leaving behind a pore. The same structures in *Orestovia* appear to us very like sunken stomata or in some cases like the dark bodies or 'grossorgane' of Kräusel and Venkatachala (1966). No evidence of 'capsules' or stomata exists for the Canadian *Spongiophyton*.

Rhytidophyton superficially seems most similar to *Spongiophyton* but apparently consists of radially symmetrical tubular thalli with pronounced vertical folding. The thalli are up to 0·6 cm wide and dichotomize, with the resultant branches forming a U-shaped pattern. One or more hemispherical protuberances 1·5–3·5 mm in diameter occur just below the dichotomy, or singly elsewhere on the thallus, which when lost form large pores. Capsules (or the oval apertures that remain after their disintegration) are irregularly distributed on the thallus surface. The thallus is interpreted as consisting of an outer cuticle, a middle fibrous zone, and an inner region of coal. *Voronejiphyton* Istchenko and Istchenko (1981), based on a few specimens, is very similar to *Rhytidophyton*, apparently differing in exhibiting occasional longitudinal ridges and internal wall thickening. In addition to lacking 'capsules', *Spongiophyton* lacks obvious folds and exhibits a single-layered thick cuticle. Its short vertical branches usually are more extensively developed or larger than those of *Rhytidophyton* and are not located at points of branching.

Orestovites is similar to *Orestovia*, differing only in rather minor features, such as the presence of several cuticle layers, hemispherical structures, major cracks in the cuticle and an irregular pattern of cells on the inner cuticle surface.

Other thalloid Devonian plants

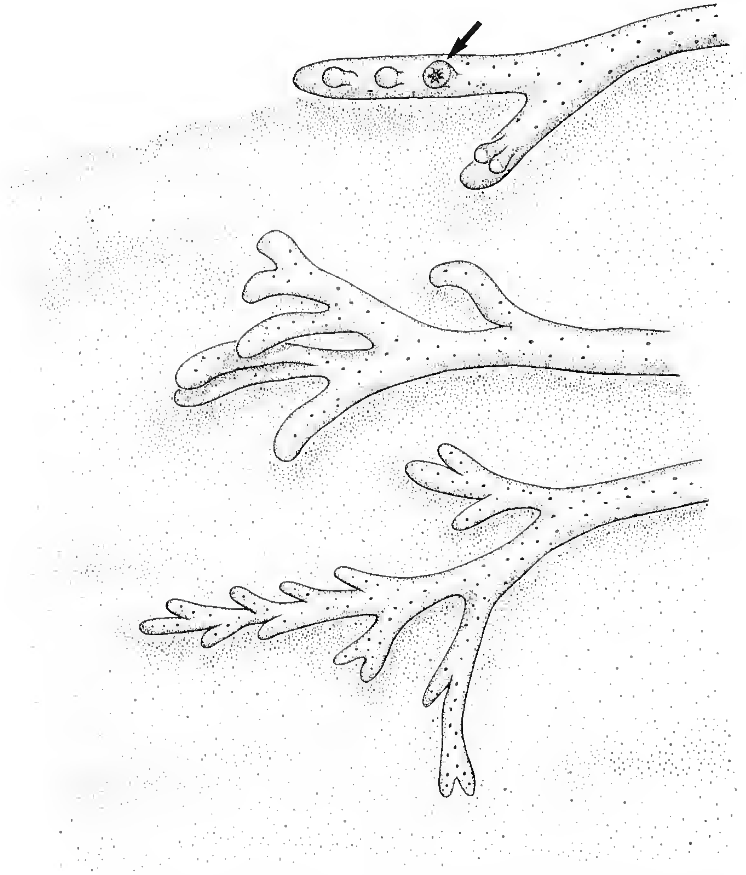
Chaloner *et al.* (1974) compared *Spongiophyton* with several other Devonian plants of thalloid construction but with one or more features attributed to land plants, e.g. *Prototaxites*, *Parka*, *Protosalvinia* and *Nematothallus*. They all differ in apparently lacking the type of tubular cuticularized thallus plus pores seen in *Spongiophyton*, *Orestovia* and *Auculeophyton* and detailed comparison of most of them is unnecessary. It is intriguing to note, however, that the vertical branches of the Canadian *Spongiophyton* resemble the proposed reconstruction of *Protosalvinia* by Niklas and Phillips (1976) even though many differences between the two taxa exist, including their postulated mode of growth (Niklas and Chaloner 1976). Reproductive structures are known for *Protosalvinia*.

The several types of isolated cuticles attributed to *Nematothallus* (sensu Edwards 1982) or *Cosmochlaena* (Edwards 1986) have been compared at times with *Spongiophyton* or other spongiophytes. These latter plants differ from *Nematothallus*, as stated by Edwards (1982), in their tubular construction and apparently parenchymatous cell structure. Further, the isolated nematophyte cuticles are not as thick as those of *Spongiophyton* and some related taxa. The original concept of *Nematothallus* was of a system of tubes covered on the upper, and perhaps lower, surface by a cuticle and possibly bearing spores among the tubes. Edwards suggested the nearly isodiametric cell outlines of the associated cuticles represented outlines of filament tips. This taxon, and *Prototaxites*, served as the basis for Lang's Nematophytales (Lang 1937). While he suggested other taxa may be included in that group, later research has shown several of them to be differently constructed. We agree with Edwards (1982) that *Spongiophyton* probably had a parenchymatous organization, which would contrast strongly with the above taxa. We also believe the term nematophyte should be restricted to plants of tubular (filamentous) construction as originally proposed by Lang, thus excluding *Protosalvinia*, the Spongiophytaceae, and probably several other enigmatic early land plants (Strother 1988).

Proposed growth habit

The extensively preserved Canadian *Spongiophyton* provides a basis for modifying concepts of its growth habit. The dorsiventral, probably cross-sectionally elliptical, tubular nature of thallus lobes is confirmed. Profuse branching, both in the same plane and at right angles, produces a growth form recalling that of some thallose liverworts such as *Conocephalum* or *Marchantia*. This extensive branching is not consistent with or feasible to the growth model proposed by Niklas and Chaloner (1976) based on studies of *S. nanum*. Whether *S. minutissimum* actually grew differently from *S. nanum* is unclear; certainly data concerning multidimensional branching were sparse at the time the model was proposed.

These specimens are found in fluvial sediments, some appearing more extensively transported than others. Their habitat may have been similar to that of many extant thallose liverworts – stream or pond margins on a flood plain. They probably formed mats or stands several centimetres to tens of centimetres broad. The stacks of thalli found at the Athoville locality document that several levels of branches may occur on a single organism, as if the older portions were partially buried and newly produced ones grew upwards (towards light?). Where thalli have been sectioned *in situ* in the matrix, the thicker (presumably upper) surface is commonly uppermost in the rock, but not consistently enough to support the possibility of the plants growing within the environment of deposition. The short vertical branches appear different from other thallus lobes, but perhaps they elongated and became more parallel to the main thallus when older, as suggested by the specimen illustrated in Text-figures 2E and 4*k*, *n*. Variation in branching and thallus orientations are depicted in the reconstruction in Text-figure 6.



TEXT-FIG. 6. Proposed reconstruction of *Spongiophyton minutissumum* plants.

The question of affinities

Despite the abundance and variety of specimens of *S. minutissimum*, many questions remain particularly on the nature of its reproductive structures and whether or not it possessed conducting tissues. This has important bearing on its affinities – particularly in relation to whether it represents an 'algal' grade of organization or one more comparable with embryophytes. It appears to be a non-vascular plant with a resistant cuticle and pores.

A resistant cuticle is generally regarded as an adaptation to a terrestrial habitat, since only terrestrial higher plants (= embryophytes) are known to possess one. Mishler and Churchill (1984,

1985) and others have postulated that a cutin-containing cuticle is a synapomorphy of the embryophyte clade. This might be further tested by chemical analysis of the cuticles of several plant types, including representatives of the charophyte-embryophyte clade, representatives of other algal clades that possess an outer covering, and of the enigmatic types discussed above. If lipid-rich (cutin-containing) cuticles occur only in the embryophytes, and if *Spongiophyton* cuticles have a similar composition, then one could place it in that lineage. The same might be true of *Orestovia* or other taxa of enigmatic affinity.

Thus, although the thalloid, presumed parenchymatous construction of *Spongiophyton* has led workers to suggest it is related to algae, one could also envision it representing an algal-derived form that had not yet attained the grade of complexity of bryophytes or vascular plants. Its affinity to the charophyte-embryophyte clade *sensu* Mishler and Churchill (1984, 1985) remains uncertain as it is possible that several extinct lineages, derived from any of several algal clades, may have become adapted for terrestrial existence and possessed a resistant cuticle. More fossils of these enigmatic types, and careful analysis of all aspects of morphology and chemistry, might address these questions. Documenting all combinations of adaptations to a terrestrial existence among Silurian-Devonian plants promises to reveal more fully the intricate story of invasion of the land by plants and of diversity of lineages at that time.

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TEUTHID CEPHALOPODS FROM THE UPPER JURASSIC OF ANTARCTICA

by PETER DOYLE

ABSTRACT. Two teuthid cephalopods, *Trachyteuthis* cf. *hastiformis* (Rüppell) and muensterellid gen. et sp. nov., are described from the Nordenskjöld Formation (Upper Jurassic) of the northeastern Antarctic Peninsula. These specimens, the only recorded teuthids from Gondwana, are closely related to European species and suggest a more widespread distribution in the Late Jurassic than was previously known.

DURING the Antarctic summer of 1987–1988 two fossil teuthid specimens were collected by the author from the Nordenskjöld Formation, a late Jurassic–early Cretaceous black shale sequence exposed in the northeastern Antarctic Peninsula (Text-fig. 1). These specimens represent the only known teuthids from any of the Gondwana continents, and as such are of importance to our understanding of teuthid distribution.

Teuthids (= Vampyromorpha of Bandel and Leich 1986 and Engeser 1988*b*) are rare fossils given the relative abundance of other fossil cephalopods (ammonites and belemnites). A survey of the teuthid fossil record shows that these cephalopods are most commonly preserved in fine-grained sediments deposited under anoxic or otherwise restricted conditions, and the present specimens are no exception. Lower Jurassic specimens are commonest, especially from the widespread Toarcian black shales of Europe (Posidonienschiefer, Jet Rock, e.g. see Riegraf *et al.* 1984; Engeser 1988*b*; and Doyle 1990 for summaries), and North America (Fernie Formation, e.g. Hall 1985; Hall and Neuman 1989). Exceptionally well preserved specimens are also known from the Middle Jurassic (Callovian) Oxford Clay of England (e.g. Donovan 1983), and similar-aged anoxic sediments in the Ardèche, France (Fischer and Riou 1982). Upper Jurassic teuthids are well represented in the Solenhofen Limestone of southern West Germany (Crick 1896; Bandel and Leich 1986; Engeser 1986) and in the Kimmeridge Clay of England (Owen 1855; Hewitt and Wignall 1988). Cretaceous restricted facies have also yielded teuthids: from the Lower Aptian 'Tock' of northern West Germany (Engeser and Reitner 1985), the Santonian Fish Bed of the Lebanon (Woodward 1883; Roger 1946; Engeser and Reitner 1986), and the Upper Cretaceous Niobrara Formation (Kansas) and Pierre Shale (Manitoba) of North America (e.g. Miller and Walker 1968; Nicholls and Isaak 1987).

The relative paucity of teuthid specimens has lead to an anomalous distribution pattern. Thus, apart from the specimens found in anoxic sediments in the United States, Cuba (Schevill 1950), the Lebanon, and the Cape Verde Islands, West Africa (Reitner and Engeser 1982), the majority of specimens are from Europe (see Engeser 1988*b*). Prior to the present study, teuthids were unknown from Gondwana, as the only record from Queensland, Australia (Moore 1870) has been found to be an indeterminate bivalve fragment (Engeser and Phillips 1986). The purpose of this paper is to document the new record and discuss its implications for palaeobiogeography.

GEOLOGICAL SETTING

From late Jurassic to early Tertiary times the northern Antarctic Peninsula was an active volcanic arc formed by the southeastward subduction of the proto-Pacific plate. During subduction, a 5–6 km thick sedimentary sequence was deposited in a retro-arc basin (the Larsen Basin) to the east of the arc. The Nordenskjöld Formation is a distinctive sequence of air-fall ashes and black

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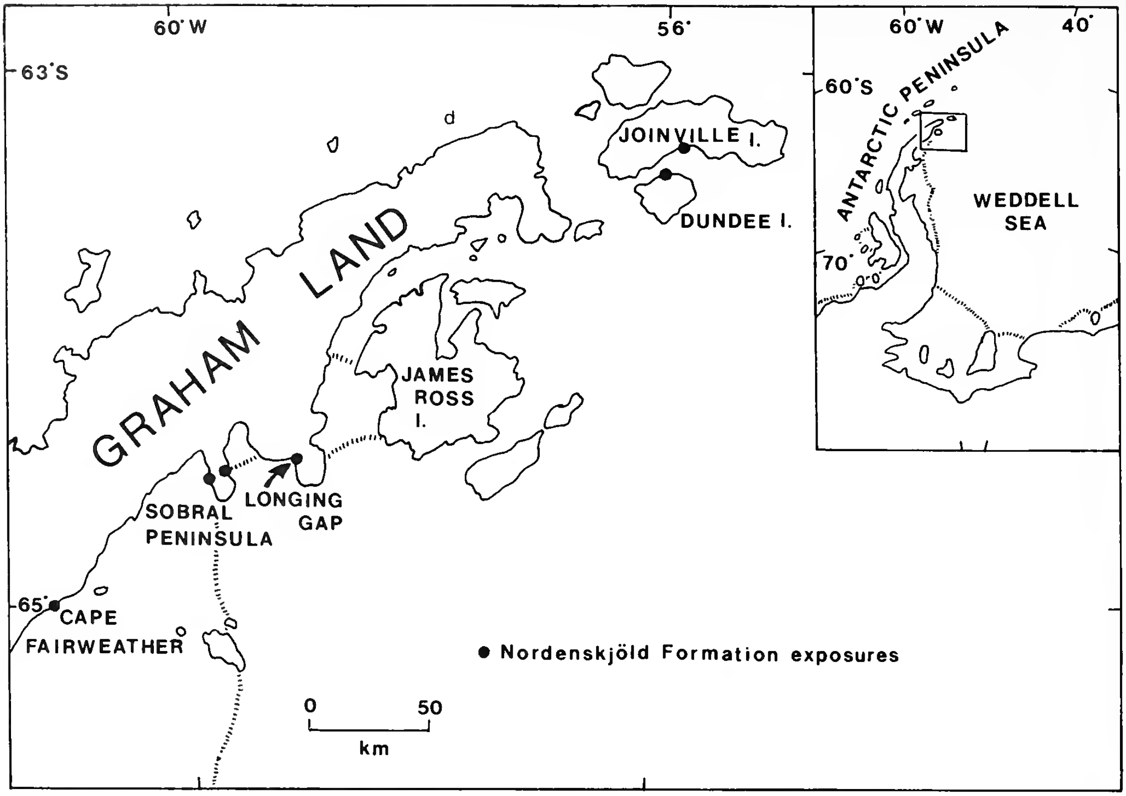


TEXT-FIG. 1. Locality map for the northeastern Antarctic Peninsula, showing the distribution of known Nordenskjöld Formation exposures. The specimens described below were collected from the type locality at Longing Gap.

mudstones of late Jurassic to early Cretaceous age which is thought to form the base of the Larsen Basin succession (Macdonald *et al.* 1988). The Nordenskjöld Formation is exposed at five localities along the northeastern coast of the Antarctic Peninsula (Farquharson 1983; Text-fig. 1), and its stratigraphy has recently been revised by Whitham and Doyle (1989).

Two members are recognized within the Nordenskjöld Formation at Longing Gap, the type locality for the formation (Text-fig. 1). The Longing Member ranges in age from Kimmeridgian to Tithonian and is dominated by parallel-laminated black mudstones with subordinate, thin ash layers. The Ameghino Member ranges in age from Tithonian to Berriasian and is characterized by structureless mudstones and thicker ash layers (Whitham and Doyle 1989). A detailed sedimentological study of the Nordenskjöld Formation is currently being carried out by Dr A. G. Whitham (British Antarctic Survey).

Both teuthid specimens were obtained from near the top of the Longing Member at Longing Gap. They were associated with a fauna consisting of the ammonites *Virgatosphinctes* spp. and *Lithacoceras* sp., and the bivalves *Retroceramus* spp. and *Arctotis* sp., of Tithonian age (Whitham and Doyle 1989). Sedimentological (parallel lamination, etc.) and palaeoecological (low faunal diversity, a lack of true benthos and trace fauna) indices show that the Longing Member was deposited under low oxygen, anaerobic to episodically dysaerobic conditions (Doyle and Whitham in press). Although the Longing Member fauna had a primarily pelagic or pseudoplanktonic mode of life, the teuthids were collected from an interval with some benthic colonization, though lacking bioturbation, suggesting dysaerobic rather than the anaerobic zone conditions characteristic of the lower part of the member (Doyle and Whitham in press).

SYSTEMATIC PALAEONTOLOGY

The terminology used below is discussed in detail in Jeletzky (1966), and the classification largely follows that of Engeser (1988*b*) (see discussion below). Both specimens are housed in the collections of the British Antarctic Survey (BAS) in Cambridge. Comparative material was examined in the British Museum (Natural History) (BMNH), London. Annotation of synonymy lists follows the convention of Matthews (1973).

Subclas COLEOIDEA Bather, 1888
Order TEUTHIDA Naef, 1916

Remarks. Jeletzky (1966) employed the order Teuthida Naef, 1916 for all known fossil squid. However, Bandel and Leich (1986) studied in detail specimens of the Solenhofen teuthids *Leptoteuthis*, *Plesioteuthis* and *Trachyteuthis*, and concluded that they possessed only eight arms, linked by basal webs, and were therefore most closely related to the Recent cephalopod *Vampyroteuthis*. This lead to the adoption of the order Vampyromorpha Robson, 1929 for all fossil 'teuthids' by Berthold and Engeser (1987), Engeser and Bandel (1988) and Engeser (1988*b*), and the contention that the fossil 'teuthids' were not directly ancestral to the Recent Teuthida. The more conservative usage of the order Teuthida Naef, 1916 is maintained below, however, as the specimens discussed below shed no further light on this discussion.

Suborder MESOTEUTHINA Naef, 1921
Family TRACHYTEUTHIDIDAE Naef, 1921
Genus TRACHYTEUTHIS Meyer, 1846
(= *Coccoteuthis* Owen, 1855, *Voltzia* Schevill, 1950; junior subjective synonyms)

Type genus. Septa hastiformis Rüppell, 1829, by subsequent designation (Bülow-Trummer 1920, p. 248).

Diagnosis. See Naef (1922, p. 137).

Remarks. The form of *Trachyteuthis*, and its relative similarity to the present-day cuttlebone of *Sepia officianalis*, has led some authors to consider that this genus is actually representative of the Sepiida rather than the Teuthida. Schevill (1950) described a new genus from the Oxfordian of Cuba, *Voltzia*, which he considered distinct from *Trachyteuthis*, as it apparently possessed 'phragmocone deposits' similar to those of *Sepia*. Donovan (1977) questioned the distinction of the nominal genera *Voltzia* and *Trachyteuthis*, but went further in suggesting that *Trachyteuthyis* was a true sepiid, attributing the lack of phragmocone to solution of the delicate aragonite plates after burial. In one specimen of *Trachyteuthis* from Solenhofen (BMNH 83730), Donovan reported fragments attributable to phragmocone debris as a 'lag' beneath the shell After sectioning, I found that this specimen revealed no further debris beneath the dorsal shield, and no indication of an extensive phragmocone development, and as such this evidence is not unequivocal. No traces of phragmocone were found in the Antarctic specimen, which is preserved as a thin shield < 1 mm thick, built of successive lamellae. An ink sac is present in this specimen, and though slightly displaced, it is found directly beneath the thin gladius, without any trace of intervening phragmocone plates.

Hewitt and Wignall (1988) have studied the mineralogy of *Trachyteuthis* specimens from the English Kimmeridge Clay, and have determined that its original mineralogy was francolite, rather than aragonite. These authors used this as additional evidence against sepiid affinities of *Trachyteuthis*, arguing that one would expect a sepiid 'cuttlebone' to be aragonitic, rather than phosphatic. The Antarctic specimen described below is also phosphatic, but the possibility of diagenetic replacement of original aragonite cannot be ruled out, especially since specimens of the thin-shelled ammonite *Haploceras* and belemnoid ?*Belemnoteuthis* (both originally aragonitic) are found as crushed, phosphatic films in the Nordenskjöld Formation.

In summary, it seems probable that despite the close morphological similarities between the shells of *Trachyteuthis* (= *Voltzia*) and *Sepia*, the absence of a proven phragmocone and the possible original phosphate shell mineralogy of the former suggest that assignment to the Teuthida rather than to the Sepiida is more correct.

Range. Definite records from the Lower Oxfordian to Tithonian of southern West Germany (Bavaria), England (Dorset, North Yorkshire), USSR (Volga region), Cuba (Viñales region) and Antarctica (Graham Land). A single doubtful record from the Lower Aptian of northern West Germany (Heligoland).

Trachyteuthis cf. *hastiformis* (Rüppell, 1829)

Text-figs 2A, B and 4

cf. *1829	*Sepia hastiformis* Rüppell, p. 9, pl. 3, fig. 2.
cf. v. 1855	*Coccoteuthis latipinnis* Owen, p. 124, pl. 7.
cf. v. 1896	*Coccoteuthis hastiformis* Rüppell; Crick, p. 439, pl. 14.
cf. 1922	*Trachyteuthis hastiformis* (Rüppell); Naef, p. 137, text-fig. 51.
cf. v. 1977	*Trachyteuthis* sp. Donovan, p. 32, text-figs 8 and 9.
cf. v. 1988*a*	*Trachyteuthis hastiformis* (Rüppell); Engeser, p. 82, text-fig. 1*c*.
cf. 1988*b*	*Trachyteuthis hastiformis* (Rüppell); Engeser, p. 59. [Full and extensive synonymy given].
v. 1988	fossil teuthid; Anonymous, p. 15, text-fig. 6. [Colour photograph of specimen described below].

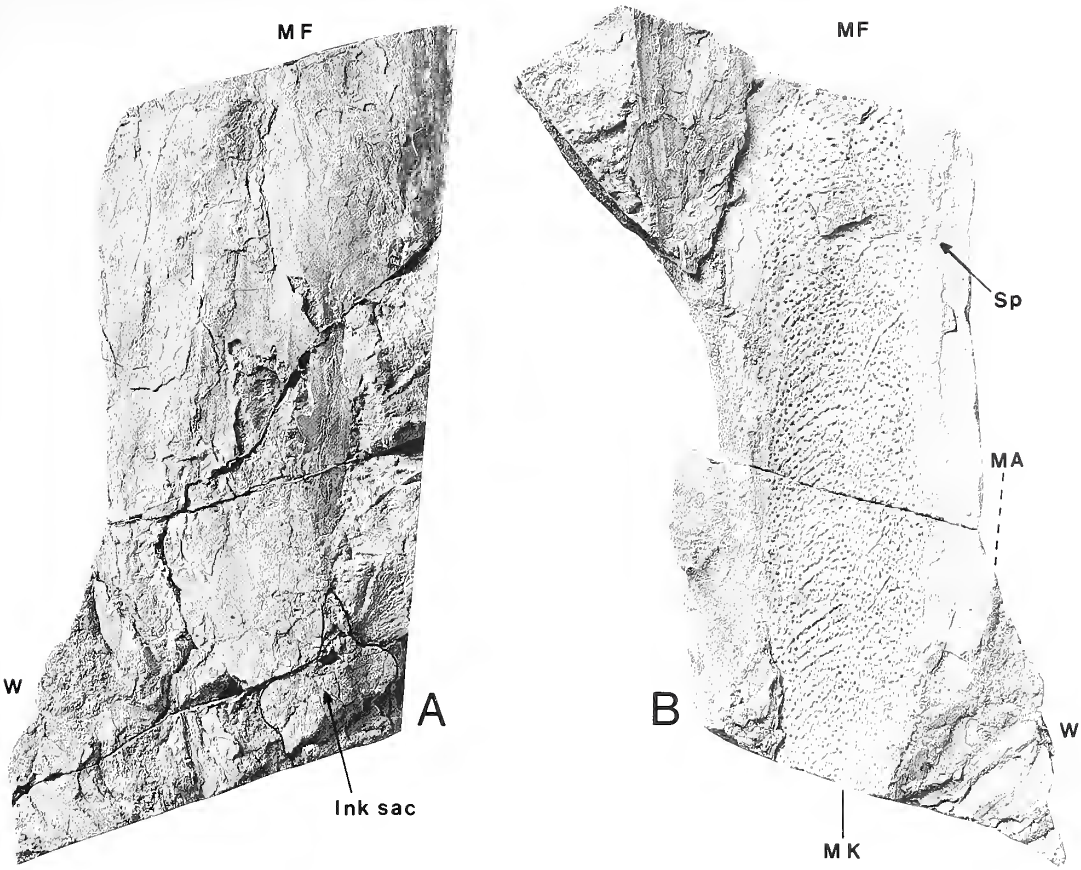
Type specimen (of *Trachyteuthis hastiformis*). Holotype, Senckenberg Museum, Frankfurt-am-Main, register number XI 1328. Lower Tithonian, Solenhofen Limestone, Mühlheim, Bavaria, West Germany.

Material. One specimen, BAS D.9007.33, uppermost Longing Member, Nordenskjöld Formation (Whitham and Doyle 1989, p. 6). Longing Gap, Graham Land, Antarctic Peninsula. Preserved intact in a carbonate concretionary horizon yielding the ammonite *Virgatosphinctes rotundidoma* Uhlig of Tithonian age (Whitham and Doyle, 1989, text-fig. 6*f*).

Description. The single specimen collected comprises the majority of the median field of a small (total preserved length 90·5 mm) *Trachyteuthis* gladius. It is preserved in a carbonate concretion allowing three-dimensional preservation, in a formation that otherwise yields compressed fossils. The specimen consists of two parts, naturally split by freeze-thaw action. These represent ventral and dorsal surfaces of the gladius divided cleanly along shell lamellae, the two parts united are less than 1 mm thick.

The dorsal fragment (Text-fig. 2B) is the most recognizable of the two as *Trachyteuthis*. It exhibits (in negative, as it is the undersurface of the topmost part of the gladius) a median field with a narrow (width 23·4 mm) central region composed of a series of closely spaced pustules arranged in arcuate arrays which correspond to growth lines. A central ridge or median keel is present. The median field is completed by relatively smooth lateral areas ('*Seiteplatte*' of Naef 1922, text-fig. 51). These are incomplete, but display some longitudinal striation. Finally, there are displaced fragments of a probable wing present at the left posterior of the shell.

The ventral fragment (Text-fig. 2A) is less easily recognizable as representative of *Trachyteuthis*, as there are no pustules or definable field areas present. The fragment consists of an almost smooth shield with some traces of arcuate growth lines in the central area. Part of the lateral area of the median field is definable in the right anterior of the specimen, and fragments of a wing in the left posterior. This portion of the gladius very clearly shows the lamellar construction of the gladius and, where successive lamellae have exfoliated, neither it nor the underlying matrix displays any evidence of phragmocone deposits. The presence of an ink sac is indicated by a dull black mass up to 5 mm thick beneath the ventral portion of the gladius in the right posterior of the fragment (Text-fig. 2A).



TEXT-FIG. 2. *Trachyteuthis* cf. *hastiformis* (Rüppell). Specimen D.9007.33, Tithonian, Longing Member, Nordenskjöld Formation, Longing Gap. Ventral and dorsal fragments of naturally split gladius, × 1. A, ventral fragment showing the ink sac beneath the thin lamellae of the shell. B, dorsal fragment showing the characteristic pustules of the median field. Abbreviations: MA, median asymptote; MF, median field; MK, median keel; Sp, '*Seiteplatte*'; W, wing. A reconstruction of the gladius is given in Text-figure 4.

Remarks. This specimen is clearly representative of the genus *Trachyteuthis*, and is very close to specimens from the Kimmeridge Clay of England and the Solenhofen Limestone of West Germany. However, its small size, which may indicate that it is a juvenile, and its incomplete preservation, allow only tentative assignment to the species *Trachyteuthis hastiformis* (Rüppel). *Trachyteuthis palmeri* (Schevill) (Lower Oxfordian, Cuba) and *T. zhuravlevi* Hecker and Hecker (Lower Volgian, Volga region, USSR) are poorly known, and differ only in their greater width and elongate form, respectively.

Suborder KELAENINA Starobogatov, 1983
Family MUENSTERELLIDAE Roger, 1952
MUNSTERELLID gen. et sp. nov.

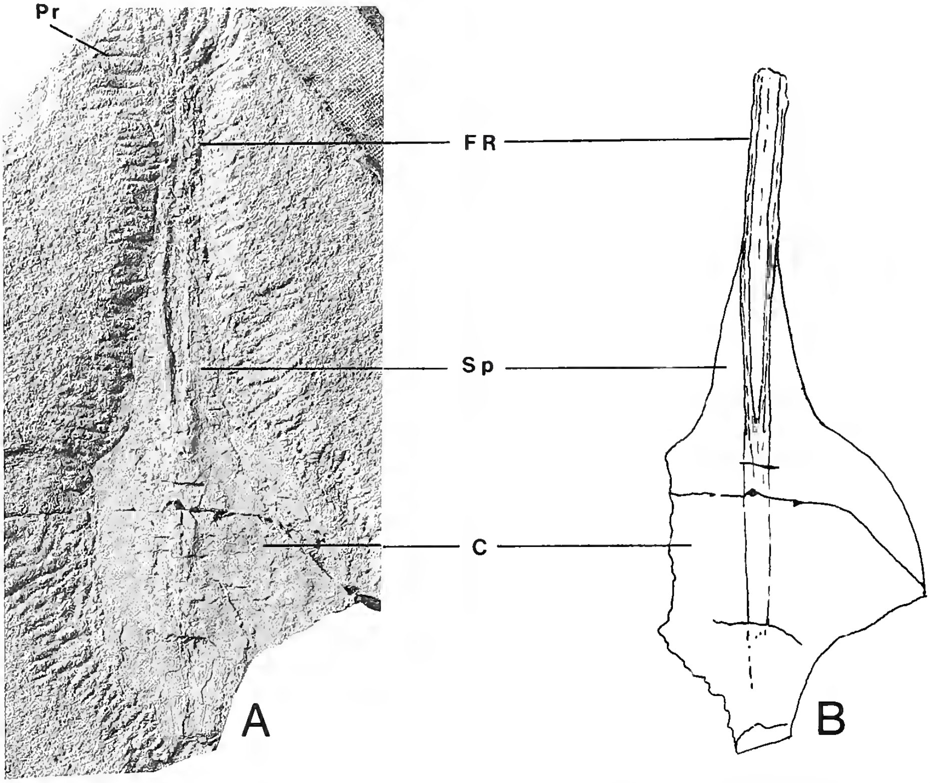
Text-figs 3A, B and 4

Material. A single specimen, BAS D.9008.3, found loose in the uppermost Longing Member (approximately equivalent horizon to BAS D.9007.33), Nordenskjöld Formation, Longing Gap, Graham Land, Antarctic Peninsula. Associated *Virgatosphinctes* and *Retroceramus* specimens indicate a Tithonian age.

Description. The specimen consists of a gladius with a preserved length of 82.5 mm, comprising a broad spoon-shaped conus with a rhachis extending anteriorly from it (Text-fig. 3A).

The spoon-shaped conus is incomplete, but has an approximate maximum width of 37 mm. It is preserved flattened with no indications of concentric or other growth lines upon its dorsal surface. The median field of the gladius is developed as a rhachis, commencing as a median ridge or raised area in the posterior of the gladius, then extending anterior of the conus. The median field is completed by smooth lateral outgrowths ('*Seiteplatte*') which accompany the rhachis for half of its length and up to 60 mm of the total length of the gladius, and indistinct surface features on the conus indicate the possible position of the median asymptotes which border the median field (Text-fig. 4).

The rhachis diverges anteriorly at an angle of approximately 5°, and expands to a maximum width of 4 mm. As the rhachis expands, it divides anteriorly from its original raised area on the conus to produce two laterally placed ridges with an intervening, smoother area. There is some indication of a weak median keel in the centre of this region, but preservation is too poor for this to be unequivocal.

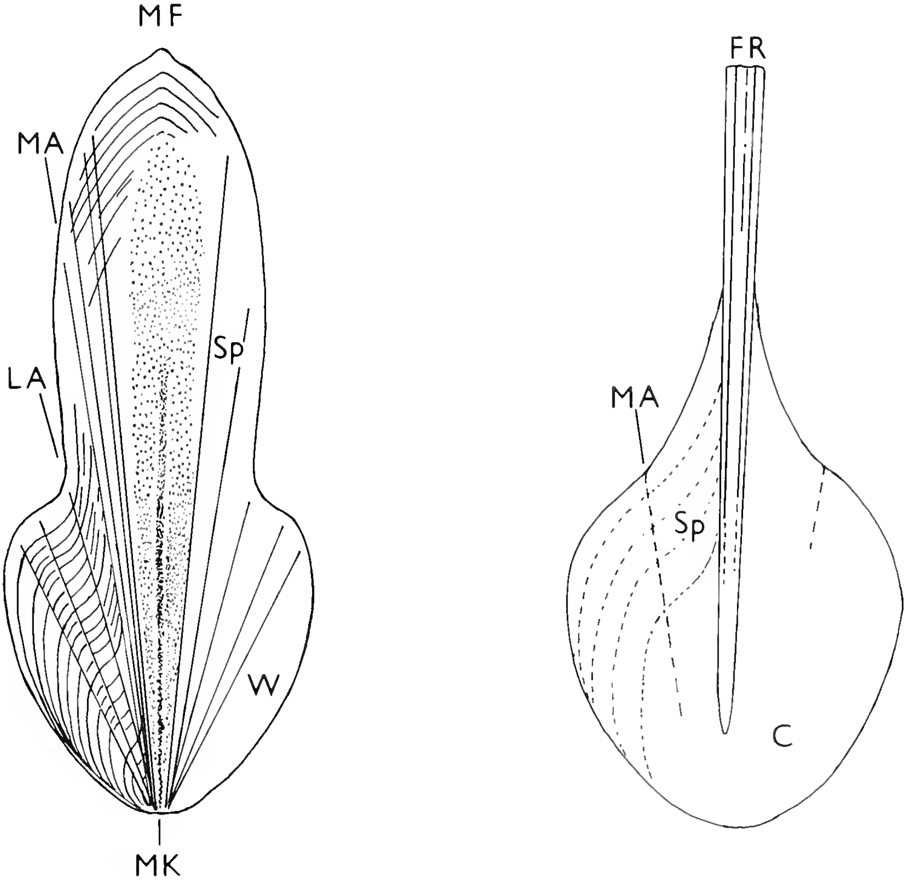


TEXT-FIG. 3. Muensterellid gen. et sp. nov. Specimen D.9008.3, Tithonian, Longing Member, Nordenskjöld Formation, Longing Gap. A, dorsal view of gladius × 1. B, sketch representation of same view, × 1. Abbreviations: C, conus; FR, free rhachis; Pr, preparation marks; Sp, '*Seiteplatte*'. A reconstruction of the gladius is given in Text-figure 4.

Remarks. The unusual divided form of the rhachis, and apparent absence of growth lines in this specimen, initially gave rise to doubts about its actual cephalopod affinities. However, despite this, the regular form of the conus and its relationship with the rhachis confirm that this specimen undoubtedly represents a (new) teuthid taxon, and it is certainly not representative of any known non-cephalopod mollusc, plant (cf. Engeser and Phillips 1986) or even fish (P. Forey, pers. comm. 1987).

The form of the specimen discussed most closely resembles taxa of the Muensterellidae (Kelaenina). Specifically, the presence of a 'free rhachis' distinguishes it from otherwise similar specimens of *Palaeololigo* Naef (Palaeologinidae, Mesoteuthina), which have a broader median field. Of the Muensterellidae, the Tithonian genera *Listroteuthis* Naef and *Muensterella* Schevill are closest, especially the former which has a similar conus shape. The only other muensterellid with a divided rhachis is the Campanian form *Tusoteuthis* Logan (= *Kansasteuthis* Miller and Walker; see Nicholls and Isaak 1987, p. 734). The gladius of *Tusoteuthis* has a leaf-shaped conus with a robust 'free rhachis' starting immediately from its anterior. The rhachis does not diverge significantly to the anterior, and is much more robust than that of the present specimen. Difference of rhachis design in otherwise similar spoon-shaped gladii of Recent squid was noted by Toll (1988), illustrating the potential for variability in this feature. The rhachis of the Recent family Bathyteuthidae would seem to be analogous to the Antarctic specimen, having lateral rods joined by a central U-shaped area.

The only Prototeuthina which approaches the present specimen is the genus *Maioteuthis* Reitner and Engeser (Plesioteuthididae). *Maioteuthis* has a much reduced conus and an extremely long and



Trachyteuthis

Muensterellid

TEXT-FIG. 4. Suggested reconstructions of the Antarctic teuthids, not to scale. *Trachyteuthis* redrawn after Naef (1922, fig. 51). Abbreviations: C, conus; LA, lateral asymptote; MA, median asymptote; MF, median field; MK, median keel; Sp, '*Seiteplatte*'; W, wing.

narrow median field which divides anteriorly to present a weak median keel (Reitner and Engeser 1982, text-fig. 2). The Antarctic specimen resembles *Maioteuthis* only in having a divided median field with a faintly developed median keel, but differs greatly in possessing a spoon-like conus with an anteriorly extensive 'free rhachis', demonstrating its muensterellid affinities.

In summary, the overall form of the gladius (conus and rhachis) of this specimen would support the erection of a new genus within the Muensterellidae. However, the single specimen available does not permit the formal designation of a new taxon.

PALAEOBIOGEOGRAPHICAL CONSIDERATIONS

There are too few records to provide any definite conclusions about the palaeobiogeography of Mesozoic teuthids. However, the discovery of fossil teuthid gladii from Gondwana is significant in illustrating that the present observed European bias is artificial, induced to some extent by the fragility of the remains and a greater intensity of study in western Europe. Therefore, some primary observations are presented here.

In addition to its European (England, West Germany) occurrences (see Engeser 1988*b* and references therein), the genus *Trachyteuthis* is recorded from the Lower Volgian of the USSR (Volga region) (Hecker and Hecker 1955), the Lower Oxfordian of western Cuba (as *Voltzia*) (Schevill 1950) and now the Tithonian of Antarctica. The majority of these specimens are remarkably similar to the western European representatives, especially the Antarctic example, suggestive of an almost worldwide distribution for *Trachyteuthis* in the Late Jurassic, transgressing boreal and Tethyan realm boundaries observed in other marine groups. Cretaceous trachyteuthids are represented only by a possible *Trachyteuthis* from the Lower Aptian of Heligoland (northern Germany) (Engeser and Reitner 1985) and Upper Cretaceous records from the Lebanon (e.g. *Libanonteuthis* Kretzoi) and North America (e.g. *Actinosepia* Whiteaves) (Engeser 1988*b*).

The Muensterellidae have similarly disparate geographical records. *Muensterella* and associated genera (i.e. *Listroteuthis* Naef, *Calaenoteuthis* Naef) are presently known only from the Lower Tithonian of West Germany (see Engeser 1988*b*). The Antarctic muensterellid, described from sediments of similar age, has many points in common with these European genera, and like *Trachyteuthis*, is a possible indicator of a formerly more widespread distribution. Cretaceous muensterellids are relatively rare, but there is some indication of less centred distribution pattern than is presently observed. Thus, while *Tusoteuthis* (? = *Kansasteuthis*, *Niobrarateuthis* and *Enchoteuthis*) is only recorded from the Upper Cretaceous of North America (Nicholls and Isaak 1987), two undescribed Australian teuthid specimens with affinity to *Tusoteuthis* are preserved in the BMNH collections. These specimens, from the Lower Cretaceous (Albian) of Queensland, Australia, (BMNH C.59211, C.59276) resemble *Tusoteuthis*, but are larger, possessing a ribbed conus and multiple grooved free rhachis, and undoubtedly represent a new taxon.

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A NEW SCLERACTINIAN-LIKE CORAL FROM THE ORDOVICIAN OF THE SOUTHERN UPLANDS, SCOTLAND

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ABSTRACT. New, discoidal fossils preserved as moulds from the middle Ordovician (Caradoc) of the Southern Uplands are shown to possess characteristic coralline microarchitecture. They are solitary, zoantharian corals with cyclic, hexameral septal insertion. Successive cycles are arranged in a system of nested triads similar to patterns associated with septal substitution in scleractinian corals. The corallum lacks tabulae or dissepiments but is epithecate with the point of origin a basal disc as in Scleractinia rather than a cone as in Rugosa. The new coral is named *Kilbuchophyllum discoidea* gen. et sp. nov., and is placed in the new family Kilbuchophyllidae and the new order Kilbuchophyllida. It is interpreted as an early example of skeletal acquisition by the group of anemones that ultimately gave rise to the Scleractinia in the Middle Triassic. The phylogeny of the Zoantharia is briefly discussed in the light of this new material.

A STRIKING feature of the geological distribution of fossil corals is the sequential ranges of the two major and crudely homoeomorphic groups possessing well developed septa. The Rugosa appear in the mid-Ordovician and become extinct at the end of the Permian (Scrutton 1979, 1988; Hill 1981), whilst the Scleractinia first occur in the middle Triassic and persist to the present day (Wells 1956; Oliver 1980). No early Triassic corals are known. The fundamental distinction between these two groups of corals lies principally in their modes of septal insertion, serial in four quadrants in the Rugosa, and cyclic, hexameral in the Scleractinia (Oliver 1980). Other zoantharian corals occur in the Palaeozoic but are less comparable. The small, enigmatic Devono-Carboniferous order Hexacorallia is also strongly septate but distinct in septal pattern from both Rugosa and Scleractinia (Hill 1981). A third major group of exclusively Palaeozoic and colonial corals, the Tabulata, have variably and generally weakly developed septa for which no definite pattern of insertion has yet been established. Claimed rugosan insertion in *Agetolites* (Kim 1974) requires restudy before its significance can be assessed. In addition, pre-Ordovician beds have yielded a small number of coralline organisms, one of which, *Cothonion*, has well developed septa and may derive from the same stock as the Rugosa (Scrutton 1979; Jell 1984).

Although direct descent of the Scleractinia from the late Palaeozoic Rugosa has been claimed by Schindewolf (1942) and others, the alternative view that the Scleractinia evolved independently from anemone precursors in the middle Triassic has been strongly argued by Oliver (1980). Over the years, a number of Palaeozoic corals had been described as exhibiting scleractinian characters. However, Hill (1960) noted that 'all Palaeozoic corals claimed...to be Scleractinia have subsequently been proved to be Rugosa...'. The sole uncertainty she allowed was the record of apparent Permian age of species of the genus *Omphalophyllia* by Minato (1955). This Japanese material is too poorly preserved to be reliably interpreted and its restudy is required; Minato (1955, p.180) considered the possibility that it was related to *Lophocarinophyllum*. On the other hand, the host rock is now interpreted as an olistostrome in a Triassic accretionary complex containing Carboniferous, Permian and Triassic olistoliths; thus there are no positive data to support Permian *Omphalophyllia* (Makoto Kato pers. comm.). The type material of *Omphalophyllia* is a Triassic scleractinian coral, considered a synonym of *Conophyllia* by Wells (1956). Since then, the possibility of a scleractinian presence in the Palaeozoic has continued to be raised. Krasnov (1970) considered Scleractinia of fungiid type to have separated from the Rugosa in the early to mid Palaeozoic with

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the Calostylidae as the most likely ancestral group. However, Smith (1930) had already shown *Calostylis* to have rugosan septal insertion and this was confirmed by Weyer (1973). More recently, Erina and Kim (1980) considered the Ordovician *Sumsarophyllum* and their new genus *Tjanshanophyllia* to both show fungiid characteristics on the basis of many cycles of perforate septa and the reported lack of an epitheca. They did not demonstrate cyclic, hexameral septal insertion, however, which must be considered the critical evidence for rejecting classification with the Rugosa and supporting comparison with the Scleractinia. Oliver (1980) concluded at that time that no known Palaeozoic coral demonstrated cyclic septal insertion.

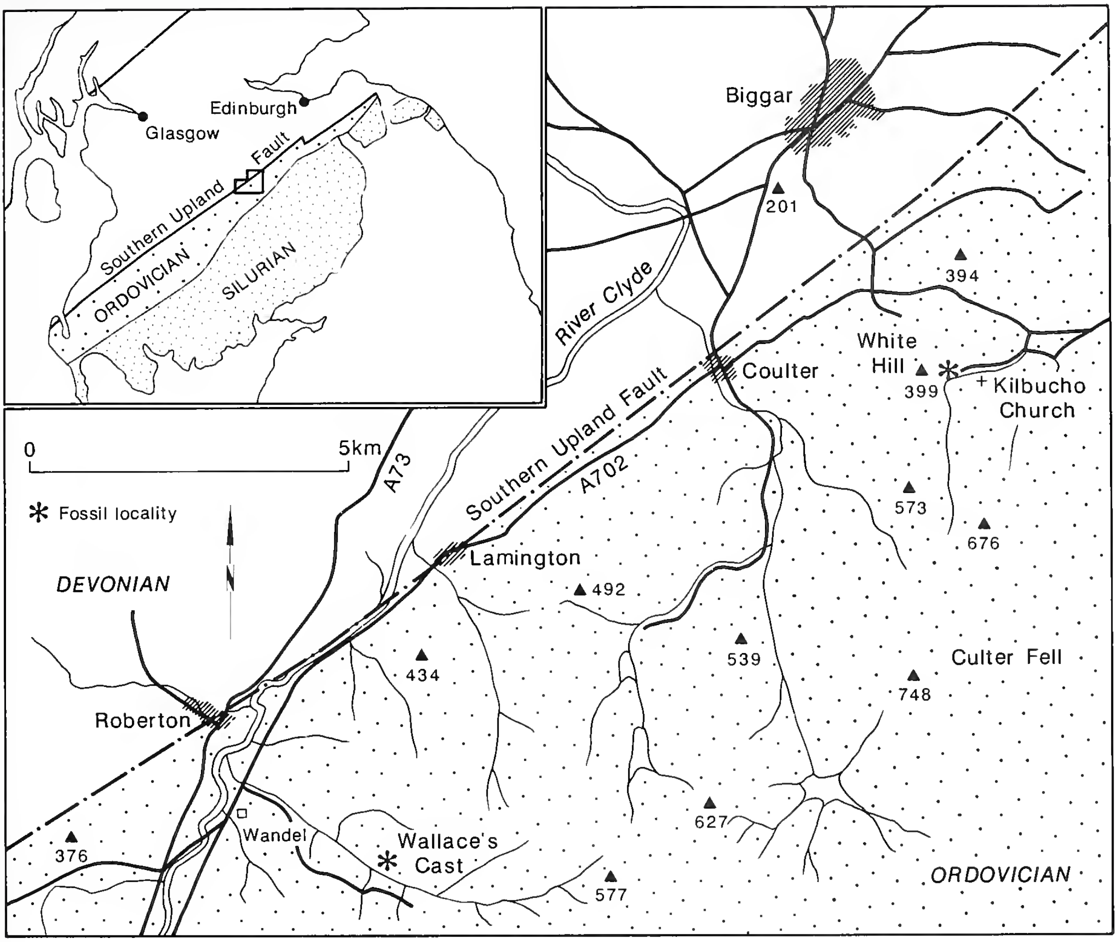
Thus we regard our description here of a new Ordovician solitary coral with scleractinian characteristics as the first well documented case of a Palaeozoic scleractiniamorph. Our claim is based on a full assessment of the structure and development of the coral, including and principally, the clear expression of hexameral cyclic septal insertion. We presuppose our conclusions concerning the nature of this material and scleractinian coral terminology is used throughout for the morphological descriptions (Wells and Hill 1956).

Abbreviations. All material we have collected is housed in the Royal Museum of Scotland, Edinburgh (RMS). Additional material referred to is housed in the British Geological Survey, Edinburgh (BGS) and The Natural History Museum, Department of Zoology, London (BM(NH)Z).

FIELD OCCURRENCE

In the Southern Uplands of Scotland, Ordovician rocks extend as a continuous belt from the North Sea to the Irish Sea (Text-fig. 1). They are largely confined to the Northern Belt and consist in the main of Arenig volcanics overlain by a suite of younger sediments. The oldest sediments are Llanvirn-Llandeilo red and grey cherts; these are succeeded by black shales of Glenkiln age (*gracilis* and *peltifer* Zones), overlain in turn by Caradoc greywackes, grits and shales. Whereas all these sediments are typically of deep-water origin, there are a number of localities, referred to by Peach and Horne (1899), which have yielded shelly fossils. The best exposures are at Kilbucho (National Grid Reference NT 060338) and at Wallace's Cast in the Wandel Burn (NT 967263) (Text-fig. 1). Other occurrences were noted by Ritchie and Eckford (1935) westwards to Duntercleuch and Snar, north-west of Leadhills.

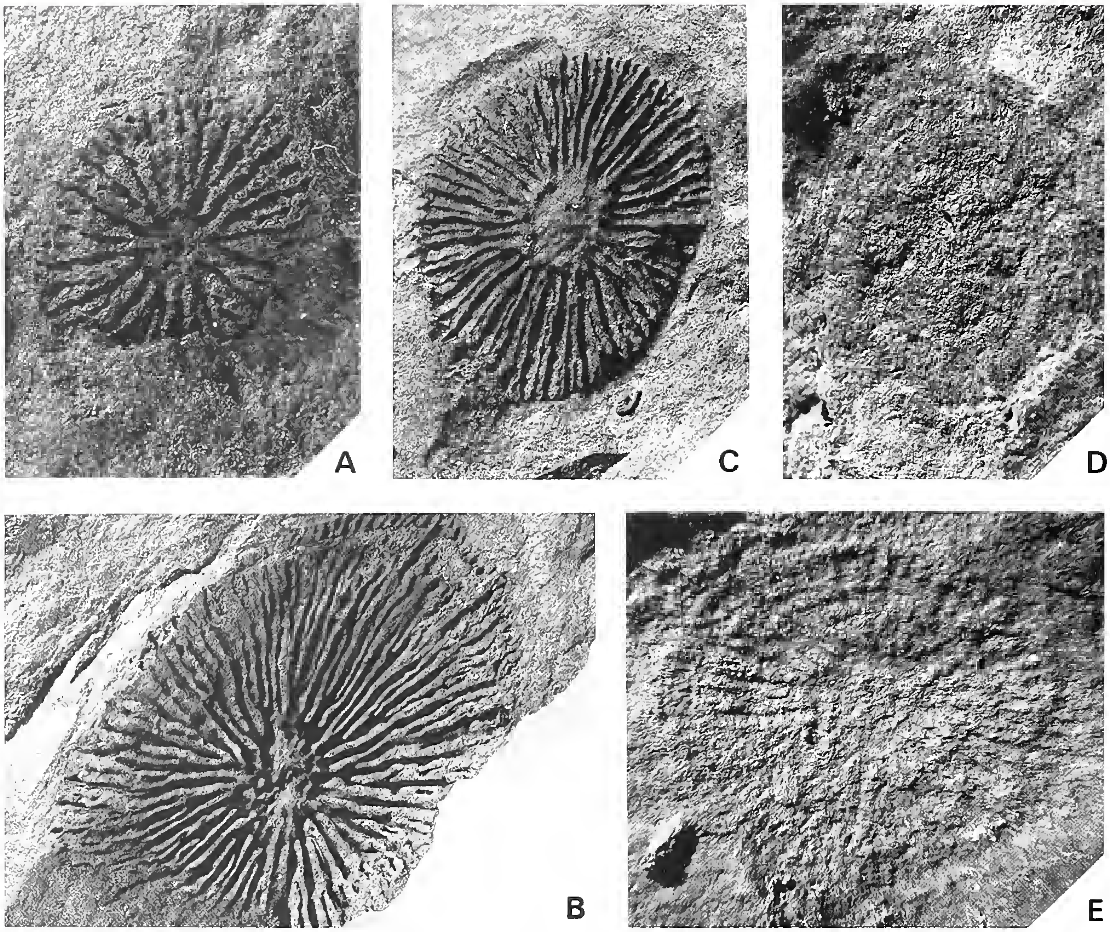
At Kilbucho and Wallace's Cast, imperfectly exposed though they are, basal greywackes are overlain by a coarse conglomerate with clasts of igneous rock, limestone and mudstone with undistorted fossils. This conglomerate fines upwards into siltstone turbidites and mudstones, cleaving subparallel with the bedding, which yield a rich assemblage of fossils, usually found in a rather distorted state. The total thickness of the conglomerates and associated siltstones and mudstones is no more than 5 m. These sediments are interpreted as debris-flow deposits, probably triggered seismically. They were originally laid down in shallow waters, following which, large unstable masses of partly and unlithified sediments slumped rapidly into deep-water, burying their faunas in the process. The sediments at the two localities of Kilbucho and the Wandel Burn are very similar, though they lie 12 km apart along the strike. It is quite possible that they record the events of a single debris flow of vast size although this cannot be confirmed. They could, on the other hand, have been smaller, separate, but near contemporaneous debris-flows from the same source. All the fossils are well-preserved as moulds (Text-fig. 2A–D), though distorted and not infrequently cracked, possibly during transportation or through diagenetic effects. The fossiliferous mudstones and siltstones are a classic obrution deposit, the fossils often being preserved at an angle to the bedding. A full description of the localities and other faunas is in preparation (Clarkson, Harper, Owen and Taylor in prep.). As well as a rich variety of brachiopods and trilobites, there are also bryozoans (especially common at Wallace's Cast), ostracodes, bivalves, gastropods, nautiloids and crinoids in addition to the material described here. Scattered solitary rugose corals are present at Wallace's Cast and rarely in mudstone clasts in the conglomerate at Kilbucho. The new genus described here



TEXT-FIG. 1. Map of the mid-north Southern Uplands of Scotland indicating collecting sites at Kilbucho and Wallace's Cast. Area of detailed map located in inset.

is known only from two poor fragments from Wallace's Cast but is common in a wide range of ontogenetic stages in a coarse-silt grade turbidite at Kilbucho, where it appears not to be associated with rugose corals.

The graywacke group in which the Kilbucho-Wandel Burn sequence occurs lies within Tract 2 of the Southern Uplands (Leggett *et al.* 1979) and belongs to the Kirkcolm Formation (J. Floyd pers. comm.). The trilobite fauna is fairly diverse, there being twelve species (A. Owen pers. comm.), and there are up to twenty-four species of brachiopods (D. A. T. Harper pers. comm.). Amongst the trilobites, the most common faunal elements are the mid-Caradoc (Balclatchie and Ardwell) *Calyptaulax brongniartii* (Portlock) (see Clarkson and Tripp 1982) and *Illaenus convergens*, with subsidiary *Stenopareia*, *Cybeloides*, *Paraharpes* and *Remopleurides*. The numerous brachiopods are very similar to those of the Bardahessiagh Formation, Pomeroy, Northern Ireland (Mitchell 1977), of high Ardwell age, but some of the elements are also found in the Balclatchie and Ardwell Beds at Girvan. The total age range of the Kilbucho-Wandel faunas cannot for the moment be dated more accurately than mid-Caradoc (Soudleyan – Actonian).

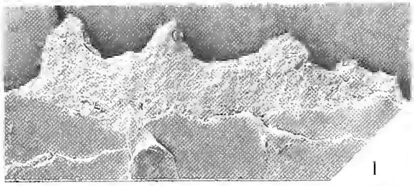


TEXT-FIG. 2. *Kilbuchophyllia discoidea* gen. et sp. nov. Ordovician, mid-Caradoc, Kilbucho, near Biggar, southern Scotland. A–D, original moulds; A, RMS 1989.36.2, calical surface of immature specimen in which septa are weakly linked spines (compare with Text-figs 3E, F); axis of symmetry vertical, × 5; B, RMS 1989.36.1 (holotype), calical surface of mature specimen in which septa are solid blades (compare Text-fig. 3G, H); axis of symmetry vertical, × 2·5; C and D, RMS 1989.36.7, calical surface; undersurface of epitheca, part and counterpart, × 3. E, RMS 1989.36.8, latex replica of external surface of epitheca showing well developed interseptal grooves and growth ridges, × 4.

EXPLANATION OF PLATE 1

Figs 1–8. *Kilbuchophyllia discoidea* gen. et sp. nov.; all scanning electron micrographs of gold coated latex replicas; Ordovician, mid-Caradoc; Kilbucho, near Biggar, southern Scotland. 1 and 2, RMS 1989.36.4, mature septal blade, corallum axis to left; note pattern of diverging columnar units in fractured face in fig. 2; 1, × 15; 2, × 60. 3, RMS 1989.36.5, oblique view of individual trabecular spine set on internal surface of epitheca at peripheral margin of corallum, × 150. 4, RMS 1989.36.2, plan view of pair of trabecular spines in mid septum, × 150. 5 and 6, RMS 1989.36.6, external surface of epitheca, periphery of corallum bottom right; 5, general view showing prominent septal grooves and growth ridges, × 15; 6, detail of growth ridge crossing interseptal ridge, × 45. 7, RMS 1989.36.4, pattern of nested triads developed about third order septum in centre of figure; first order septum to left of group, second order septum to right of group, × 15. 8, RMS 1989.36.5, papillose axial structure of merged trabecular spines, × 30.

PLATE 1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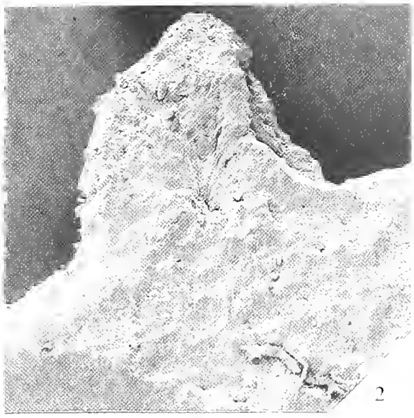
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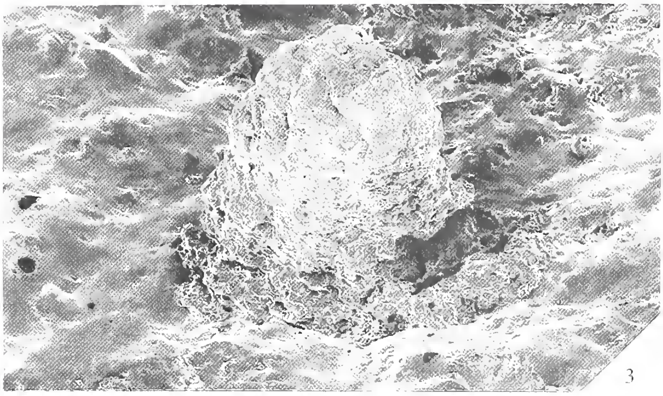
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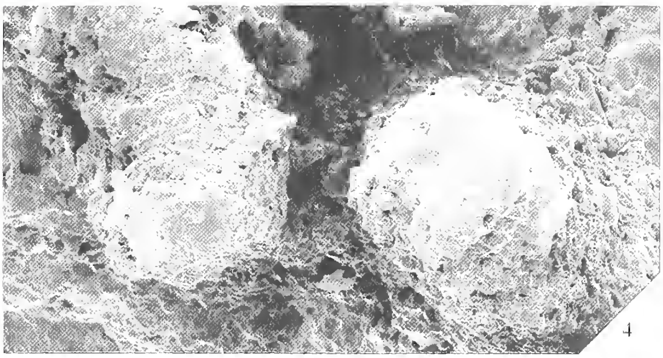
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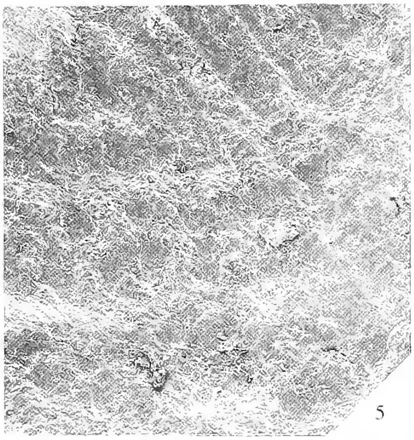
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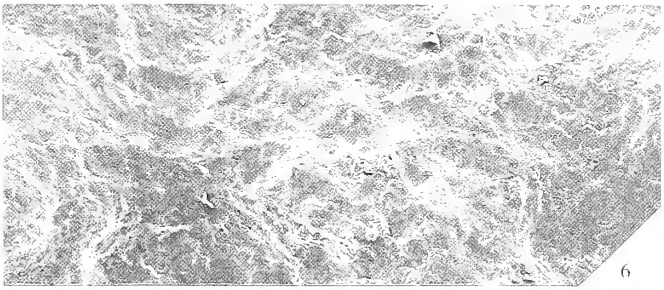
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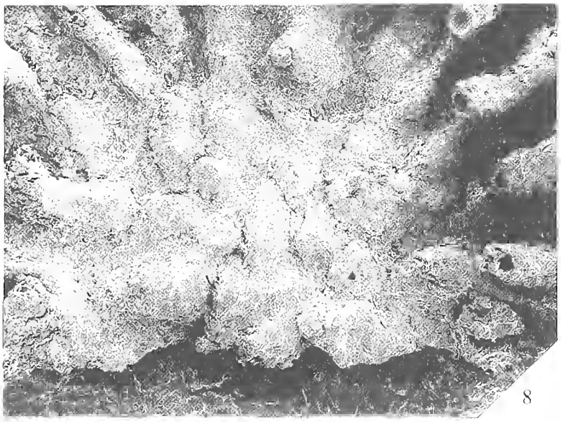
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SCRUTTON and CLARKSON, *Kilbuchophyllia*

PREPARATION

The mouldic material, preserved in a coarse-silt grade, quartz-rich turbidite with a substantial mica and clay mineral matrix, was cleaned in a weak solution of Calgol in an ultrasonic bath and latex replicas were made using standard techniques. Although these replicas demonstrate overall three-dimensional appearance of the coral, distortion of the septal blades, either taphonomic or tectonic, tends to obscure the detailed interseptal relationships in most specimens. Therefore, septal patterns were traced directly from the moulds using a camera lucida attachment on the microscope. These reflect the growth of the septal blades on the upper surface of the epitheca and are thus likely to reflect the interseptal relationships most accurately. For the purposes of illustration in Text-figure 3, these patterns have been reversed to show the standard calical view of septal arrangement in corals.

The latex replicas were used for SEM study of septal microarchitecture. Selected replicas were coated with gold under vacuum to a thickness of 12–15 nm and examined at a range of magnifications using a Cambridge Instruments Stereoscan 240 in the Biomedical E.M. Unit at the University of Newcastle upon Tyne. Problems of creep in the latex were solved by working at low energy levels, between 0·5 and 4 kV. Very low magnification pictures taken at settings for maximum depth of field, such as that in Text-figure 3H, suffer from slight spherical distortion but have been preferred for their clarity over light microscope photographs.

In coral studies, mouldic preservation is usually regarded as of limited value. It is less of a disadvantage in the present material because of the discoidal growth form and lack of horizontal elements between the septa: no macrostructural detail is lost. However, the SEM results obtained here, suggest that all mouldic material may repay closer examination.

MORPHOLOGICAL CHARACTERISTICS

A full description of this new species is given below. The present discussion concentrates on the two most important features bearing on the anthozoan cnidarian nature of the material and its phylogenetic relationships within the class: microarchitecture of the skeletal elements and septal pattern.

Microarchitecture

SEM study of gold-coated latex replicas reveals the preservation of elements of about 20 μm and above in the better preserved material. Individual septal spines of up to 200 μm diameter, in specimens RMS 1989.36.2 and 5, are constructed of upward and outwardly diverging columnar units of indeterminate length and subrectangular to rhomboidal to irregular (?oblique) section, *c.* 20 μm across (Pl. 1, figs 3 and 4). Viewed from above, terminations give the appearance of overlapping roof tiles, possibly helically arranged in a conical stack. Where spines are first linked to form continuous but beaded septal plates, the intervening ridges are composed of units of similar size and shape. In larger coralla, in which individual spines have been subsumed into dentate, flat faced septal blades, the lateral faces of the blades have the appearance of a uniform fabric of overlapping scales (Pl. 1, figs 1 and 2). On the fractured surface of a septal tooth, internal upward fanning of columnar units is visible; the effect of overlapping scales is produced by oblique terminations of these units at the surface. No substructure is visible within these units.

The axial structure in some smaller coralla is composed of a cluster of discrete spines (Pl. 1, fig. 8). These have the same structure as the septal spines and are clearly septal in origin.

The basal surface of the epitheca shows circumferential ridges, demarcating growth increments, and sometimes, except in the axial area, radiating septal grooves (Pl. 1, fig. 5; Text-fig. 2D,E). In between ridges, the surface is smoother and may be very smooth to almost featureless. At the ridges, a cluster of overlapping triangular to arcuate elements averaging 40 μm across forms a low scarp slope directed towards the axis (Pl. 1, figs 5 and 6). Individual elements are oriented radially and offlap towards the periphery, the ultimate series in each ridge subparallel to the inter-ridge surface of the epitheca. The calicular surface of the epitheca is rather smooth and undulating in places but elsewhere shows sub-vertically orientated elements with low pyrimidal terminations approximately 20–40 μm across. These define a fabric which appears to have a crudely radial orientation in places (Pl. 1, fig. 3).

Septal pattern

Septa are arranged radially, reaching up to 0·8 of the corallum radius in length, on a flat, circular (see below) basal disc. Pattern is most readily detected in the smaller coralla with about 30–40 septa. In larger, mature coralla, with up to 120 septa, not only are most specimens incomplete but septal arrangement becomes increasingly irregular.

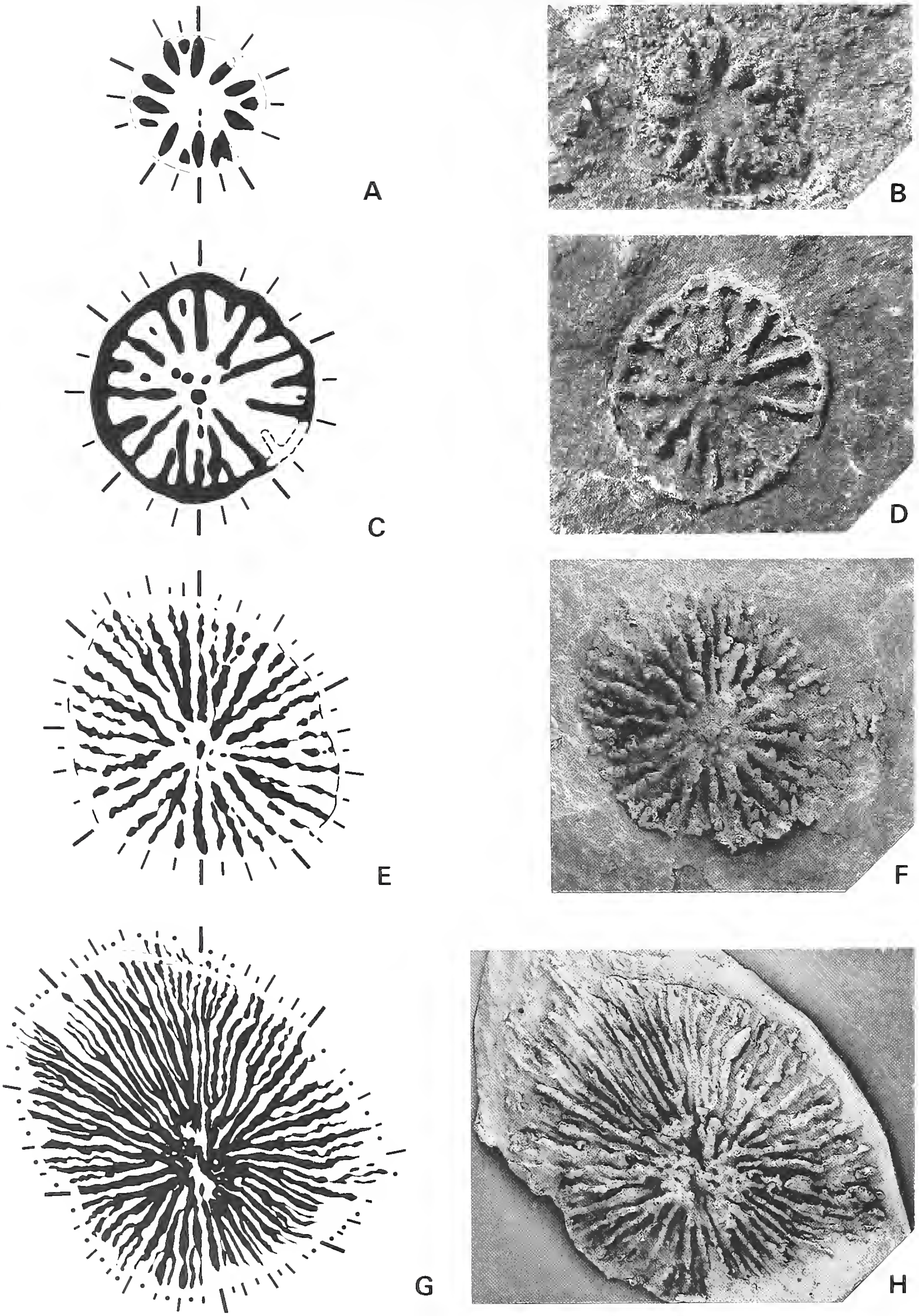
Two features reveal the septal pattern: the relative length of the septa, and curvature of the inner ends of septa of higher order to face, or rest against the flanks of septa of lower order (Pl. 1, fig. 7). In RMS 1989.36.2 (Text-figs 2A and 3E, F), 12 septa of approximately equal length extend 0·8 radius to the axis. Of these, alternate septa are each flanked by two shorter septa, between 0·5 and 0·75 radius in length, whose axial ends turn, more or less strongly, towards each other and the opposite faces of the dividing, longer septum. There are thus 12 of these shorter septa. Eight of these are again each flanked by a pair of even shorter septa, 0·1 to 0·5 radius in length and converging on opposite faces towards the axis. This repeated pattern of septal convergence leads to the appearance of nested triads of septa of which there are six, separated by six of the longest septa which have no divergent septal groups. These latter are interpreted as six first cycle septa, alternating with six second cycle septa that form the axis of each set of nested triads. The successive groups of diverging septa represent, respectively, 12 third cycle septa and 16 fourth cycle septa, amounting to 40 septa in all. The fourth cycle here is regarded as incomplete, numbering 24 septa when complete. The two triads lacking fourth cycle septa are adjacent and flank an axis of bilateral symmetry defined by a short septal blade in the axial area of the coral.

All of the available material, except the smallest specimen, clearly shows this septal pattern of nested triads and often some weak indication of an overall bilateral aspect. Two further specimens unequivocally, and several others less certainly, demonstrate the hexameral symmetry of the pattern of triads. One, RMS 1989.36.4 (Pl. 1, fig. 7), is only slightly larger than RMS 1989.36.2 and shows complete first to fourth cycles of septa and an incomplete fifth cycle containing 10 septa. The pattern of nested triads is uncertain and probably anomalous in one sextant; the specimen is damaged at this point. A bilateral symmetry is suggested by the 5th cycle occurring almost exclusively in two opposite sextants. RMS 1989.36.1 (Text-fig. 3G, H) is close to the maximum diameter known so far for this coral. It also shows complete first to fourth cycles of septa, whilst the fifth cycle is better developed but still incomplete with 31 septa and the sixth cycle rarely developed and represented by 6 septa. Bilateral symmetry is again suggested by septal arrangement in and around the axial area and by slightly higher septal numbers in two opposite sextants. However, the numerical difference is small and peripheral preservation incomplete so that septal number may be higher than apparent.

Only two relatively immature specimens are available (Text-fig. 3A–D). No pattern of convergence is seen in the smallest specimen, RMS 1989.36.3 (Text-fig. 3A, B), and septal identity is uncertain: the interpretation shown draws on comparison with the pattern developed in larger coralla. The larger specimen shows weakly developed triads. We have been conservative in our interpretive sketch (Text-fig. 3C) and faint traces on the specimen suggest the possibility of greater axial extension of the third order septa towards the second order septa (Text-fig. 3D). The appearance of third order septa in more mature specimens suggests that some extension or strengthening of their axial ends takes place as growth proceeds.

The details of septal insertion cannot be substantiated by a study of septal grooves on the underside of the epitheca. These are only rarely well-developed and tend to fail almost completely in an axial area *c*. 4 mm across. Often the whole epitheca appears to lack septal grooves (Text-fig. 2D). Supporting evidence is limited to faint indications of peripheral triads, as at top-right in Text-figure 2E.

Many specimens show varying degrees of irregularity in insertion. However, an overall pattern emerges of a pair of adjacent sextants relatively retarded and a further pair of opposite sextants relatively accelerated. The pattern is symmetrical about the plane of bilateral symmetry where this is clear from features in the axial area of the corallum. In the smallest coralla available (Text-fig. 3A–D), retardation is already apparent in the adjacent pair of sextants (orientated towards the



TEXT-FIG. 3. For legend see opposite.

bottom of each figure). Acceleration in lateral sextants does not become marked until the insertion of the 5th cycle begins. It may be so extreme in some larger corallites that an initial impression is given of eight rather than six sets of nested triads. An idealized representation of the septal pattern in these corals is given in Text-figure 4A.

AFFINITIES AND RELATIONSHIPS

Anthozoan affinities

The gross morphological features of these specimens immediately suggest coralline affinity. The only other reasonable possibility seems to be a relationship to the Porifera, based on a crude homeomorphy with forms like *Haplistion* (Rigby 1987). No other phylum is known to produce a structure of this size range and form.

The microarchitecture of the septa clearly rules out poriferan affinity and strongly supports assignment to the Anthozoa Cnidaria. The characteristic pattern of elements in the septal spines can be matched very closely among the Scleractinia (for example, Sorauf 1972). In particular, the appearance of granulations on the lateral faces of septa in *Fungia*, representing one spherulitic cluster of crystallites (Sorauf 1972, pl. 14, fig. 5), is indistinguishable in appearance from the tips of the septal spines in the present material, although smaller in size (Pl. 1, figs 3 and 4). Granulations on the septal faces in *Cladocora* (Sorauf 1972, pl. 13, fig. 4) are also similar. The fabric on the lateral faces of septal blades (Pl. 1, figs 1 and 2) compares with that in *Fungia scutarea* (Sorauf 1972, pl. 11, fig. 2) but is much coarser. The elongate units defined in the present material are assumed to be composed of bundles of fine acicular crystals, not resolvable here either because of the limitations of the moulding medium, or recrystallization, or both. However, there seems to be sufficient evidence to establish the septal spines as trabeculate. Such microstructure appears to be characteristic of the anthozoan Cnidaria.

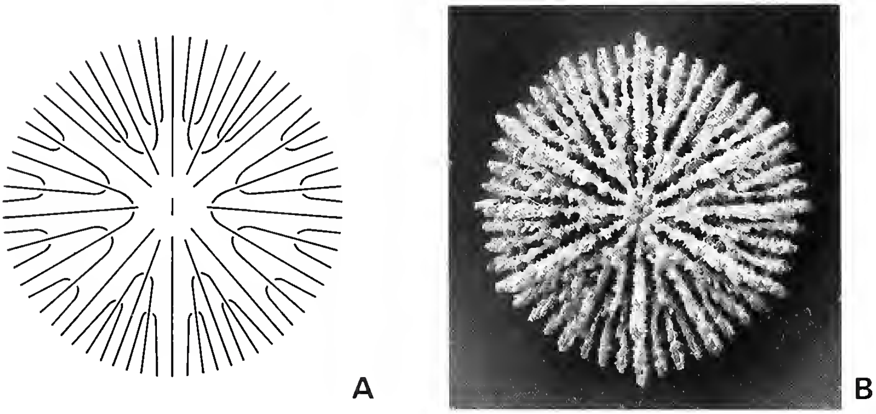
This evidence, together with the discoidal epithecate form and the radial distribution of the spinose or bladelike septa, clearly identifies this material as a zoantharian coral.

Affinities within the Anthozoa

In detail, this material is unlike any other known Palaeozoic coral, either from the established Rugosa or Heterocorallia, or the more scattered and problematic Cambrian material. It is grossly most similar to some solitary, discoidal Rugosa (for example, Hill 1981, fig. 39) but is fundamentally distinguished from them by its septal arrangement. These new specimens unequivocally show six-fold cyclic insertion in contrast to the serial insertion in four quadrants of rugose corals.. The septal development in Hexacorallia, based on four primary septa (Hill 1981), is even more distinct. On the other hand, this pattern of cyclic insertion is indistinguishable from that in scleractinian corals (Vaughan and Wells 1943; Wells 1956; Jell 1980; Oliver 1980). The tendency for cycles, particularly above the third, to be incomplete when higher cycles are initiated is common in Scleractinia. The evidence of bilateral symmetry is also seen in septal development in many scleractinians and, as pointed out by Oliver (1980), is a reflection of the fundamental radiobilateral symmetry of all known anthozoans. A dorso-ventral polarity in the insertion of septal cycles is a feature of some scleractinians (Vaughan and Wells 1943; Wells 1956; Oliver 1980) and we interpret the relative retardation of a pair of sextants in the present material to indicate the equivalent of the ventral pole

TEXT-FIG. 3. *Kilbuchophyllia discoidea* gen. et sp. nov. Ontogenetic series, Ordovician, mid-Caradoc, Kilbucho, near Biggar, southern Scotland. Photographs (B and D) and scanning electron micrographs (F and H) of latex replicas of calical surfaces are matched with interpretive sketches based on information from original moulds and corresponding replicas. Plane of bilateral symmetry vertical, supposed dorsal pole at top. Septal cycle indicated as follows: protosepta, long heavy lines; 2nd, 3rd and 4th cycles, successively shorter light lines; 5th cycle, spots; 6th cycle, unornamented. A and B, RMS 1989.36.3, × 8. C and D, BGS 9936, × 8. E and F, RMS 1989.36.3, × 6. G and H, RMS 1989.36.1 (holotype), × 2·5.

in scleractinians. In conformity with scleractinian usage, we have orientated the presumed dorsal pole uppermost in the material described here. However, we are not aware of relative acceleration in the pair of opposite sextants in scleractinians.



TEXT-FIG. 4. A, *Kilbuchophyllia discoidea* gen. et sp. nov. Idealized reconstruction of septal pattern. Plane of bilateral symmetry vertical with supposed dorsal pole uppermost. B, *Fungiacyathus symmetricus* (Pourtalès). BM(NH)Z 1880.11.25.123, Recent specimen, collection station details uncertain, ×4.

The distinctive pattern of nested triads of second and higher orders of septa is similar to a version of Portalès Plan which is developed in some scleractinian corals. Pourtalès Plan is regarded as a reflection of septal substitution during ontogeny, when the peripheral ends of exosepta split to accommodate subsequent entosepta. Vaughan and Wells (1943, p. 34) stated that it may be assumed that substitution has occurred when septa of a higher cycle unite with those of a lower cycle. A range of patterns of uniting septal ends is possible in detail, but the arrangement in the present material is remarkably similar to that exhibited by such Scleractinia as *Fungiacyathus symmetricus* (Text-fig. 4B; Vaughan and Wells 1943, pl. 34, figs 1*a* and 4) and *Balanophyllia* (*Eupsammia*) *zelandiae* (Squires 1958, p. 73, fig. 28). However, this is not identical to the classic pattern in dendrophyllid corals illustrated by Vaughan and Wells (1943, fig. 13) and Wells (1956, fig. 239) in which the entosepta are less well-developed than the exosepta. Also the pattern in the present material is equivocal. The axial septum of a triad is usually more or less structurally continuous and the flanking septa bend towards but do not always touch or merge with the axial septum. This does not immediately suggest the process of substitution. In some cases the peripheral ends of existing septa are deflected around the tips of newly inserted septa, at this stage a string of septal spines, in a manner suggesting substitution. However, we cannot be certain that these instances are not irregularities in insertion rather than clues to its character. If septal splitting did occur, the appearance of septa in the smaller specimens suggests that it was unlikely to have affected either the first or second orders. It seems also that further work is needed on the origin of some of the patterns attributed to Pourtalès Plan in living corals. Thus it is premature to claim septal substitution as occurring in this Ordovician material.

This very close similarity to the Scleractinia is reflected in other features. The origination of septa as discrete spines, subsequently linked by thin blades of material to give a beaded appearance to the septa, is very reminiscent of the early stages of skeletal development in some Recent corals (see, for example, Jell 1980). The rather confused appearance and irregularities in metasepta insertion in the early ontogenetic stages mentioned and illustrated by Jell are very similar to those seen here. Furthermore, the coarsely denticulate upper margins of the septal blades in mature coralla are also closely comparable to those seen in many scleractinian corals but are not a characteristic of the Rugosa. An epitheca or holotheca is almost universal among rugose corals but, as a well developed feature, is confined largely to some ahermatypic (mainly caryophyllid and dendrophyllid) forms among the Scleractinia. In the Rugosa and Tabulata, it appears always to develop from an initial conical structure secreted by the polyp on settlement and metamorphosis, whereas in the Scleractinia it develops on the edge of the basal disc (Jell 1980). In the present material the central area of the epitheca is featureless and flat; there is no sign of a conical stage in development (Text-fig. 2D,E). The microarchitecture of the epitheca shows similarities with that described for *Manicina* by Sorauf (1972), although the structures preserved here are much coarser in scale. Also, the character of the upper surface conforms closely in appearance to the secondary layer on the surface of the basal disc of *Porites lutea* illustrated by Jell (1980).

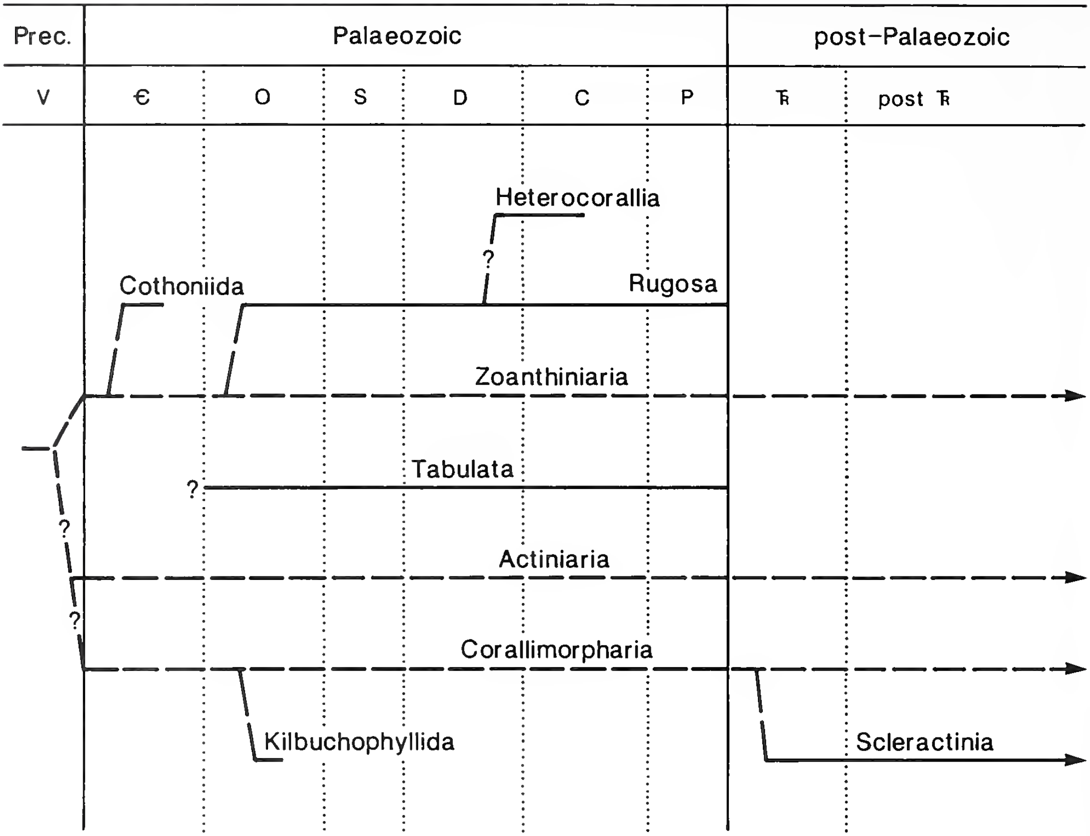
These specimens occur with a rich invertebrate fauna, preserved almost exclusively as moulds, the vast majority of which originally had calcium carbonate shells or skeletons. The skeletal material is thus assumed to have been calcium carbonate. Whether the skeleton was originally calcitic or aragonitic is much more speculative. Little is known of microarchitecture in the rugose corals, widely regarded to have been originally calcitic (Sandberg 1984), although internal ultrastructure appears to be identical to that in the Scleractinia. Sorauf (1980, p. 335) considered that biomineralization in the Rugosa closely resembled that in the Scleractinia, differing only in original mineralogy. In any case, in the material described here the finest detail of the microarchitecture is not preserved. The only evidence is indirect; similarity to the Scleractinia is so close that the original mineralogy may well have been the same, that is to say aragonitic.

Phylogenetic relationships

The evidence suggests very close affinity between this Ordovician material and the Scleractinia among the Zoantharia Anthozoa. It seems highly improbable that intermediates over a period of 220 Ma could all have escaped preservation and/or detection even if it is assumed that these corals remained ecologically confined to oceanic environments. In fact the associated organisms clearly indicate a shelf and/or upper slope fauna. It seems more probable that the Palaeozoic specimens represent an earlier, ultimately unsuccessful attempt at skeletonization by the same group of anemones that later gave rise, probably polyphyletically, to the Scleractinia. Such a conclusion requires the existence of anemones with a cyclic hexameral pattern of mesenterial insertion at least as early as the mid-Ordovician. Thus it strongly supports the rejection of the Rugosa as ancestral to the Scleractinia (Oliver 1980).

The ancestral anemone group is usually considered to be the Corallimorpharia, identical to scleractinian polyps but skeletonless (Wells and Hill 1956; Hill 1981; Oliver and Coates 1987), although Hand (1966) has suggested the possibility of the reverse relationship on functional grounds, with the Corallimorpharia and Actiniaria evolved from the Scleractinia by loss of the skeleton. The new Ordovician material, however, appears to favour the former scenario. Furthermore, if its septal pattern can be confirmed to be identical to one known to result from septal substitution in living corals, this isolated skeletonized species would itself presumably require an anemone precursor already possessing paired mesenteries. Thus the range of the Corallimorpharia, and/or the closely related Actiniaria, must be extended back at least that far to provide the same ancestral anemone stock for this and the Scleractinia. Anemones have an almost non-existent fossil record (Scrutton 1979) but it now seems possible that all the various groups of anemones may have differentiated during the initial cnidarian radiation in the late Precambrian.

A possible phylogeny for the Palaeozoic Zoantharia Anthozoa, modified after that of Oliver and Coates (1987), is given in Text-figure 5. The present material has the same relationship to the Scleractinia as the Middle Cambrian Cothoniida probably, but perhaps less certainly, has to the Rugosa (Jell and Jell 1976; Scrutton 1979; Oliver and Coates 1987). The latter are regarded as having evolved from the Zoanthiniaria, in which later mesenterial couples are inserted serially in only one pair of sextants (Wells and Hill 1956; Hill 1981). The relationships of the other major group of Palaeozoic corals, the Tabulata (taken to include the Heliolitida) is equivocal. Some or all



TEXT-FIG. 5. Phylogeny of the Anthozoa Zoantharia (modified after Oliver and Coates 1987).

Rugosa have been claimed to have direct tabulate ancestry (Flower 1961) but, although the earliest skeletal ontogenetic stage appears always to be conical as in the Rugosa, we regard this as most unlikely (Scrutton 1979; Neuman 1984). Septa are absent or weakly developed in the Tabulata and no general pattern of insertion has been demonstrated. Tabulate corallites rather seldom show bilateral symmetry; septal development is usually radially uniform and 12 septa are sufficiently common, together with a rare instance of preservation of twelve tentacled favositid polyps, for a fundamental dodecal symmetry to have been claimed for the group (Copper 1985; Mistiaen 1989). These factors suggest a corallimorpharian or actiniarian ancestor to be as, if not more, likely for this group than a zoanthiniarian ancestor among known orders of anemones, although it seems equally possible that the tabulates evolved from a separate group of anemones now extinct.

SYSTEMATIC PALAEONTOLOGY

Phylum CNIDARIA Hatschek, 1888
Class ANTHOZOA Ehrenberg, 1834
Subclass ZOANTHARIA de Blainville, 1830
Order KILBUCHOPHYLLIDA nov.

Diagnosis. As for genus.

Discussion. The Kilbuchophyllida is homoeomorphic to a high degree with the Scleractinia. However, the combination of a solitary discoidal, epithecate form lacking dissepiments, with solid, bladed septa nested in triads and more or less strongly accelerated in the lateral sextants, does not appear to occur among the Mesozoic to Cenozoic scleractinian corals. Although the combination of characters in the only known species is unique, all, with the possible exception of the pattern of septal acceleration, are individually or severally found in various scleractinians. Ultimately, the classification of this species in a new order is based on its stratigraphic separation and our presumption of lack of direct descent to the Scleractinia.

Family KILBUCHOPHYLLIDAE nov.

Diagnosis. As for genus.

Genus KILBUCHOPHYLLIA gen. nov.

Derivation of name. After the type locality, Kilbucho (pron. -bukko), near Biggar, southern Scotland.

Diagnosis. Solitary, discoidal, epithecate radiobilateral corals showing hexameral, cyclic septal insertion. Septa, spinose to solid blades, arranged in a pattern with the internal ends of higher order septa turned towards or resting against the flanks of lower order septa. Adjacent sextants (?ventral pole) with retarded septal insertion in early ontogeny, lateral sextants accelerated in later ontogeny. No dissepiments.

Kilbuchophyllia discoidea sp. nov.

Plate 1, figs 1–8; Text-figs 2, 3, 4A, 6

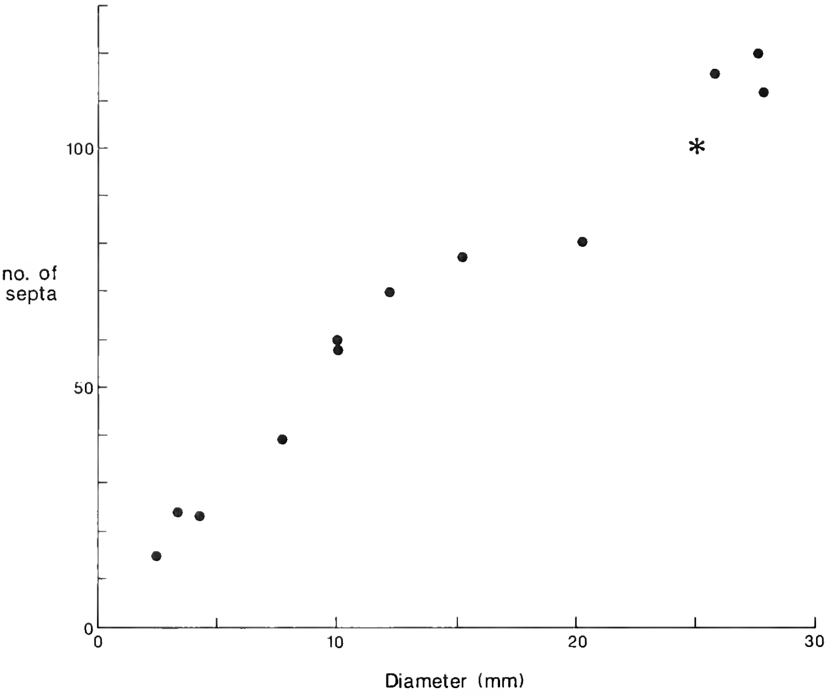
Diagnosis. Circular, solitary, discoidal corals with diameter up to 28 mm and estimated maximum 120 septa. Up to six cycles of septa of which the fourth sometimes and the fifth and sixth cycles always are incomplete. Second and higher orders involved in pattern of nested triads. Insertion retarded in adjacent (?ventral) sextants in early ontogeny, accelerated in lateral sextants in later ontogeny. Axial area with discrete trabeculae (?pali) merging to form papillose or contorted axial structure. Weak bilateral symmetry usually apparent. Epitheca a flat disc with concentric growth ridges and occasionally septal grooves. No dissepiments.

Holotype. RMS 1989.36.1. Ordovician, middle Caradoc; Kilbucho, near Biggar, southern Scotland.

Paratypes. RMS 1989.36.2–12; BGS 9936. Same horizon and locality as holotype.

Description. Solitary, circular, discoidal corals ranging from 2·6 mm diameter with 15 septa to 27·5 mm with estimated 120 septa (Text-fig. 6). In small coralla, septa either discrete trabecular spines or in lower order septa, spines linked by a low thin ridge giving septa a beaded appearance. In larger coralla, spines subsumed in smooth faced blades, *c.* 0·3 mm thick, with coarsely toothed upper margin in all but highest order septa, although less completely fused peripherally and particularly adaxially. Individual spines *c.* 0·2 mm diameter with axes *c.* 0·3 mm apart; septal teeth spaced *c.* 0·7–0·9 mm. Height of spines or septal blades 0·75–1·0 mm in smaller coralla, rising to *c.* 2·3 mm high in the largest coralla. Septal height greatest at mid length of smaller coralla, migrating to axial end of septa in larger coralla. Six first (protosepta) and six second cycle septa of more or less equal length, 0·8 radius in all but smallest coralla. Higher cycles, up to sixth, successively shorter in length. Second and higher cycles of septa involved in a pattern of nested triads, with higher cycles at their inner ends turned towards or resting against the flanks of lower cycles. The first two cycles complete in smallest available corallum, third cycle complete between 3–4 mm diameter, fourth cycle complete by about 10 mm, fifth cycle absent from smaller coralla, ?complete in largest coralla, sixth cycle variably present only in largest coralla and never complete. Septal insertion retarded in adjacent sextants (at ?ventral pole of polyp) in early ontogeny, accelerated in lateral sextants about plane of bilateral symmetry in later ontogeny. Axial area with discrete trabecular spines, ?equivalent to pali, in smallest coralla. With size increase, spine bases variably embedded to form flat or slightly arched papillose area. In one case, spines linked as extensions of septa to form dome of twisted, interlocked plates. Bilateral symmetry may be weakly defined by a more or less well-developed bladed element in axis but sometimes not obvious. Epitheca a flat disc with peripheral depth 0·3–0·5 mm high. Central area featureless and may be almost smooth throughout but concentric growth ridges usually and radiating septal grooves sometimes clearly developed around central area. There are no dissepiments.

Discussion. Except for the smallest specimens, all the material is elliptical in plan. When apparent, the plane of bilateral symmetry is not coincident with the long axis of the ellipse and the shape is due to tectonic distortion in the rock. Strain analysis yields a value of R_i of 1·06. Allowing for the difficulty of measuring axes accurately in some of the material, this suggests that the coral was originally effectively circular.



TEXT-FIG. 6. *Kilbuchophyllia discoidea* gen. et sp. nov. Plot of septal number against diameter for better preserved material. Both parameters estimated in many cases because of damage to margins of specimens. Holotype indicated by asterisk.

Variation in most features in the material available, allowing for ontogenetic stage, is relatively limited. The axial structure is the most variable aspect of mature specimens. One coral, BGS 9936, representing an early ontogenetic stage, is unique in possessing a distinct low rim linking the peripheral ends of septa. Whether or not this is aberrant, or the rim is obscured by thickening of the upper surface of the epitheca in larger coralla, is unknown.

The specimens often appear to have suffered some damage before final burial, consistent with their presence in a debris flow. In particular, the septal blades in the larger specimens are often damaged and their upper margins incomplete. Because of incomplete preservation there is an element of estimate in all the data on Text-figure 6, although the error is considered unlikely to exceed 10%.

Range. This species is known so far from some 20 specimens and fragments from the type locality. Two fragments have been recovered from similar beds of the same age at Wallace's Cast, Wandel Burn, 12 km west-south-west along strike, southern Scotland.

Acknowledgements. We are grateful to all those with whom we have discussed various aspects of this study, particularly Stephen Cairns (Smithsonian Institution, Washington, D.C.), Bill Oliver (US Geological Survey, Washington, D.C.), Makoto Kato (Hokkaido University, Sapporo), Keith Rigby (Brigham Young University, Utah), Martin Le Tissier and Graham Young (University of Newcastle upon Tyne). Susan Bruce (University College, Galway) kindly contributed the smallest specimen, which she collected. Brian Turner commented on the matrix to the specimens, scanning electron micrographs were taken by Trevor Booth and Text-figures 1, 3, 5, 6 were drafted by Christine Jeans; Peter Lewis and Brian Tuffs helped with preparation (all University of Newcastle upon Tyne). Simon Moore (Natural History Museum, London) and Peter Brand (British Geological Survey, Edinburgh) kindly arranged the loan of material in their care.

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THE TAXONOMY AND SHELL CHARACTERISTICS OF A NEW ELKANIID BRACHIOPOD FROM THE ASHGILL OF SWEDEN

by LARS E. HOLMER

ABSTRACT. A new elkaniid brachiopod genus and species, *Tilasia rugosa*, is described from the Ashgill (Harju Series) Boda Limestone in the Siljan district (province of Dalarna), Sweden. It is the first record of the lingulacean family Elkaniidae from the Upper Ordovician. The material of *T. rugosa*, which is one of the largest described member of the family, is well preserved and allows an account of the micro-ornamentation and shell structure. The strongly rugose exterior has a divaricate ornamentation with minute rhomboid pits, previously not known among the elkaniids.

ELKANIID brachiopods are common and widely distributed mainly in the Upper Cambrian and Lower Ordovician (Tremadoc-lower Llanvirn); the family has not previously been recorded from beds younger than the Middle Ordovician.

Here a new genus and species, *Tilasia rugosa* from the Upper Ordovician (Ashgill) Boda Limestone in the Siljan district, province of Dalarna, Sweden (Text-fig. 1), is described. The rare but well preserved material of this large elkaniid also permits an account of the shell structure and micro-ornamentation, not previously known from this group.

MATERIALS AND METHODS

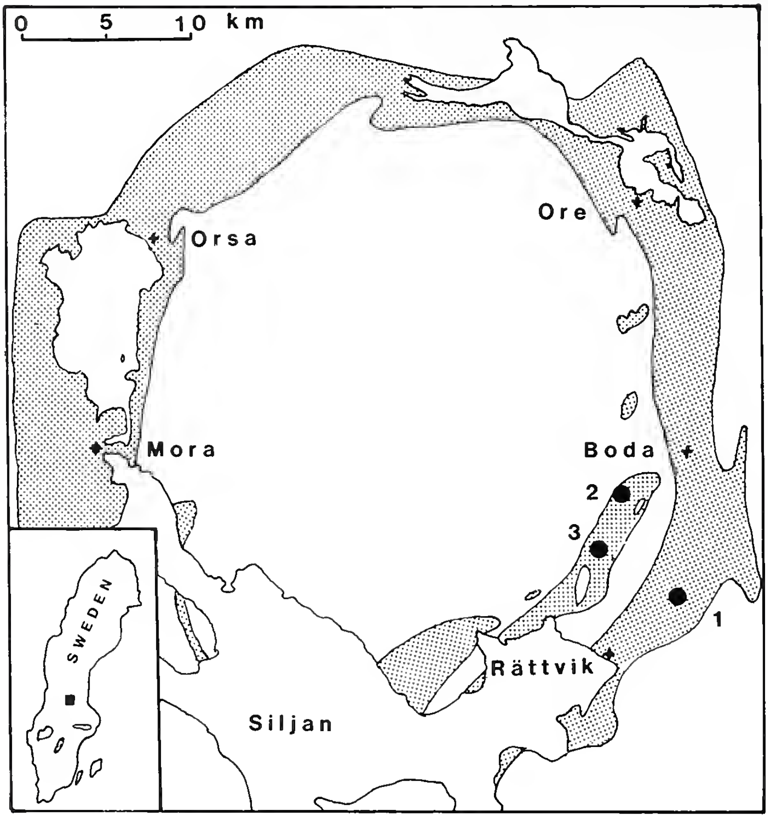
In the Siljan district, Lower Palaeozoic (Upper Cambrian? to Silurian) rocks crop out within a tectonically complex ring-structure, which probably represents a hypervelocity impact crater (Text-fig. 1; see Jaanusson 1982 for a review). The Boda Limestone (within the *Amorphognathus ordovicicus* Biozone: Bergström 1971) is a large (maximum diameter, 1000 m; thickness, 140 m), lens-shaped, stromatactis-bearing unit, with a high carbonate content. Although reef-like, it lacks an organic frame; it represents a carbonate mound, possibly comparable with modern lithoherms (Jaanusson 1979, 1982).

The phosphatic inarticulates (discinaceans) from these beds have previously been described by Lindström (*in* Angelin and Lindström 1880) and Holmer (1987). The stratigraphy and fauna of the Boda Limestone were summarized by Jaanusson (1958, 1982).

The material was prepared from the limestone by etching with 10% buffered acetic acid (see Jeppsson *et al.* 1985 for details); the outer or inner surfaces of the valves were covered with a layer of epoxy resin to avoid fragmentation during the etching process. To study shell structure, specimens embedded in epoxy resin were sectioned, polished and subsequently etched with 4% hydrochloric acid for 4 seconds; the counterparts of the sectioned valves were used to make thin sections for examination in transmitted light.

The type material is housed in the Department of Palaeozoology, Swedish Museum of Natural History (SMNH), and in the Department of Geology, University of Lund (LO). Detailed descriptions of the localities (Östbjörka, Boda, Jutjärn, and Skålberget; Text-fig. 1) in the Siljan district are given by Thorslund (1936; see also Jaanusson 1982).

[Palaeontology, Vol. 34, Part 1, 1991, pp. 195–204.]



TEXT-FIG. 1. Location map of the Siljan district, province of Dalarna, Sweden, showing the ring-structure with Lower Palaeozoic rocks (shaded) and the localities investigated (filled circles). 1, Jutjärn; 2, Östbjörka; 3, Skålberget.

SYSTEMATIC PALAEONTOLOGY

Class LINGULATA Goryansky and Popov, 1985
Order LINGULIDA Waagen, 1885
Superfamily LINGULACEA Menke, 1828
Family ELKANIIDAE Walcott and Schuchert, 1908

Diagnosis. See Rowell (1965, p. H270).

Genera assigned. *Monobolina* Salter, 1866; *Elkania* Ford, 1886; *Broeggeria* Walcott, 1902; *Lamanskya* Moberg and Segerberg, 1906 [= ?*Dictyobolus* Williams and Curry, 1985]; *Elkanisca* Havlíček, 1982; *Tilasia* gen. nov.

Discussion. The detailed morphology of many of the elkaniid genera listed above remains poorly known, perhaps partly because they have usually been described from material from argillaceous sequences (e.g. *Broeggeria*, *Monobolina*, *Elkanisca*); well preserved complete specimens from carbonates have generally not been available.

The elkaniid affinity of *Monobolina* was recently questioned by Havlíček (1982, p. 50). However, the new data on the morphology of *M. plumbea* (Salter) presented by Lockley and Williams (1981, p. 15, figs 31–34) indicates that it belongs within the Elkaniidae. Lockley and Williams (1981) also described the new species *M. crassa*, which extended the range of the family into the Middle Ordovician (Llandeilo).

The poorly known Lower Ordovician (Tremadoc) *Lamanskya* Moberg and Segerberg, 1906, from Öland, Sweden, was previously placed questionably among the Strophomenidina (Williams 1965, p. H863), but is now considered to be an elkaniid (Holmer 1989); the type (and only) species, *L. splendens* Moberg and Segerberg, is widely distributed in the Lower Ordovician of Sweden, and is currently being redescribed. The Irish Lower Ordovician genus *Dictyobolus* Williams and Curry, 1985 (type species *D. transversus* Williams and Curry), which is here referred to the elkaniids, appears to be a junior synonym of *Lamanskya* (Holmer unpublished). The likewise poorly known *Aulonotreta kuraganica* Andreeva, 1972 from the Lower Ordovician of the Ural Mountains probably also represents a new genus of the elkaniid brachiopods (L. E. Popov, personal communication 1989).

Genus TILASIA gen. nov.

Type species. *Tilasia rugosa* sp. nov.

Etymology. In honour of Daniel Tilas (1712–1772), who published the first detailed account of the Lower Palaeozoic strata of Dalarna (Tilas 1740).

Diagnosis. Large, transversely suboval, moderately and subequally biconvex, rugose shell; exterior pitted with rhomboid pits. Ventral pseudointerarea with wide propareas and deep, triangular pedicle groove; ventral umbonal muscle scar divided by anteriorly directed extension of the pedicle groove. Dorsal pseudointerarea with wide median groove and narrow propareas.

Species assigned. *Tilasia rugosa* sp. nov.;? *Obolus*? sp. 3 Cooper, 1956.

Tilasia rugosa sp. nov.

Text-figs 2–5

Holotype. SMNH Br133686, almost complete shell (width 26·6 mm, length 22·4 mm, thickness 10·0 mm) from the Boda Limestone, Jutjärn quarry, Siljan district, Dalarna (coll. M. Frye).

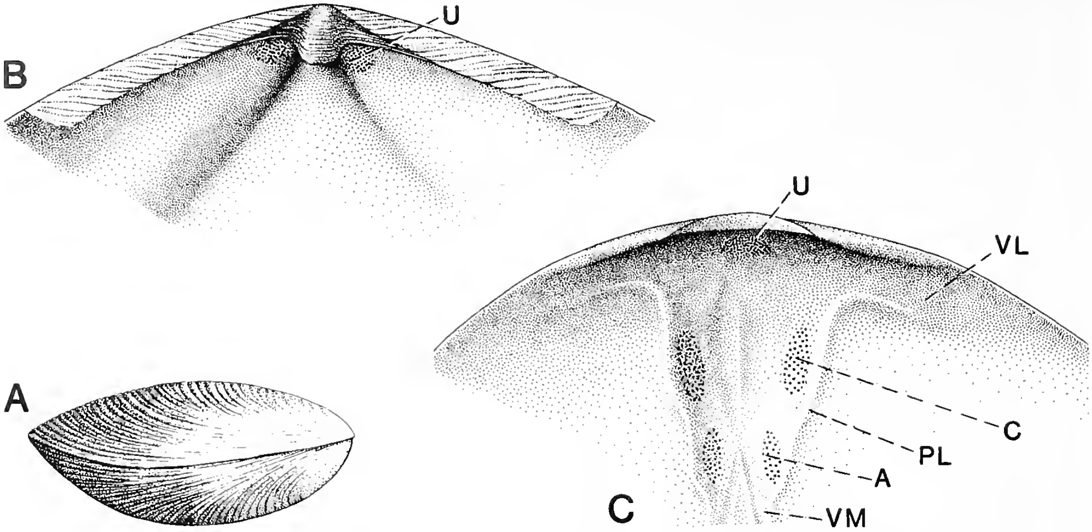
Paratypes. All material from the Boda Limestone, Siljan district, Dalarna; SMNH Br133691, incomplete dorsal valve, Skålberget quarry (coll. E. Jarvik; flank facies; locality 8 *in* Jaanusson 1982, fig. 3; SMNH Br102556*a*, incomplete dorsal valve (previously identified as fragmentary dorsal valve of *Orbiculoidea*? *gibba in* Holmer 1987, p. 320), Skålberget quarry (flank facies; coll. J. Martna); LO 5956, incomplete ventral valve, Östbjörka (coll. S. L. Törnquist); LO 5957 (not figured), incomplete ventral valve, Boda (coll. S. L. Törnquist). Total of two dorsal and two ventral valves.

Etymology. Latin *rugosus*, wrinkled; alluding to the rugose ornamentation.

Diagnosis. As for genus.

Description. Shell large (up to 26·6 mm wide and 22·4 mm long in one specimen), and moderately, subequally biconvex, 38% as thick as wide (Text-figs 2A and 3E); transversely suboval in outline. Ornamentation strongly rugose (see also below) with regularly disposed, up to 0·5 mm high rugae, on average 0·5 mm apart (Text-figs 3A, D, F, I and 4A–F).

Ventral valve (of holotype) 1 mm longer than dorsal valve, 84% as long as wide, but less convex (about 1 mm difference), 15% as high as wide (Text-figs 2A and 3A, E). Interior of ventral valve not known in detail; ventral pseudointerarea 14–16 mm wide (in two specimens), occupying 50% of valve width, with well developed propareas, 1·3 mm wide; deep, triangular pedicle groove, 4·3 mm wide and 1·6 mm long; ventral umbonal muscle scar divided by anteriorly directed extension of pedicle groove (Text-figs 2B and 4G–I). An



TEXT-FIG. 2. *Tilasia rugosa* sp. nov. A, lateral profile of complete shell, based on SMNH Br133686. B, ventral interior, based on LO 5956. C, dorsal interior, based on SMNH Br133686. All × 6. U, umbonal muscle scar; VL, *vascula lateralia*; C, central muscle scar; PL, platform; A, anterior lateral muscle scar; VM, *vascula media*.

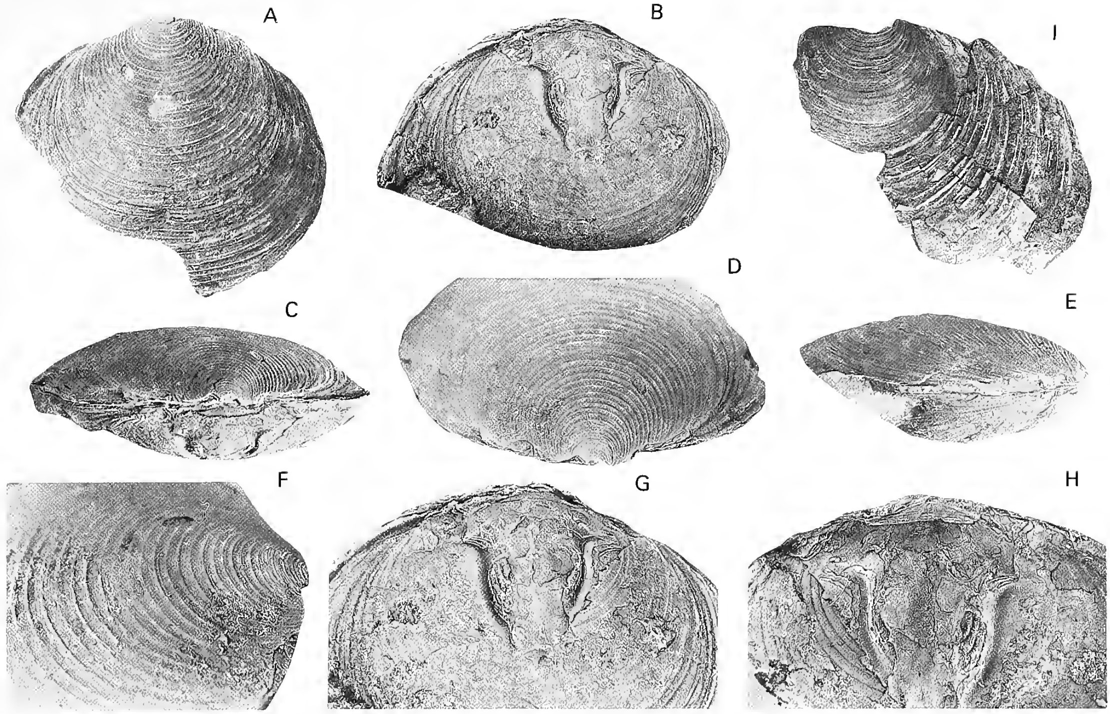
unfigured, poorly preserved fragment of a ventral valve (No. LO 5957) shows a section through an elevated platform, directly anterior to the umbonal muscle scars, but the detailed morphology of the platform is not known.

Dorsal valve (of holotype) 80% as long as wide, and 23% as high as wide (Text-figs 2A and 3B, E). Dorsal pseudointerarea with median groove, 5·6 mm wide and 0·6 mm long; exact dimensions of propareas unknown, but they appear to be narrower than the ventral ones (Text-figs 2C and 3G–H). Dorsal umbonal muscle scar situated directly anterior to median groove; central and anterior lateral muscle scars situated on an elevated, subtriangular platform, 7 mm wide and 9 mm long, with low median septum; well-developed vascular markings with *vascula lateralia* diverging anterolaterally from umbonal muscle scar, and *vascula media* diverging anterior to anterior lateral muscle scars (Text-figs 2C and 3G–H).

Remarks on ontogeny. All the examined specimens represent adults. The early ontogeny of *T. rugosa* is not known; the apical region of the valves is fragmentary. The regularly shaped, biconvex shells do not show any major interruptions or changes in the growth pattern during the juvenile and adult stages; the major concentric rugae are formed at regular intervals. In an early part of the juvenile stage (when the shell is up to 3 mm wide and 2 mm long) the rugae are densely spaced, about 0·16 mm apart; during later growth stages they become gradually more widely spaced, up to 0·8 mm apart; a fully grown shell appears to have up to about fifty major rugae (Text-fig. 3A, D, F). In some specimens there are minor, more irregular rugae between the major ones (Text-fig. 4A–C).

Discussion. *Tilasia rugosa* differs from mot other elkaniids (such as species of *Broeggeria*, *Elkanisca*, and *Monobolina*) mainly in being more biconvex and strongly rugose. It is most similar to species of *Elkania*. However, *T. rugosa* differs in being less biconvex and more rugose; the thickness of the type species *E. desiderata* (Billings) (Rowell 1965, p. H270, fig. 164: 1*a–c*) is about two-thirds of its width and most species of *Elkania*, like *E. hamburgensis* (Walcott), are smooth, having only weakly developed growth lines (Rowell 1965, fig. 164: 1*d–f*).

Lamanskya splendens Moberg and Segerberg, 1906 (p. 71, pl. 3: 17) and '*Aulonotreta*' *kuraganica* Andreeva, 1972 (p. 46, pl. 7: 1–3) differ in being more strongly biconvex; the thickness of the latter is up to three-quarters of its width; moreover, the dorsal platforms of these two species are much higher (Holmer unpublished; Andreeva 1972, pl. 7: 3).



TEXT-FIG. 3. *Tilasia rugosa* sp. nov., Boda Limestone (Ashgill), Siljan district, Dalarna. A–H, holotype, complete shell, Jutjärn, SMNH Br133686; A, ventral exterior, × 2; B, internal mould of dorsal valve, × 2; C, posterior profile, × 2; D, oblique posterior view of ventral valve, × 2·5; E, lateral profile, × 2; F, oblique lateral view of ventral valve, × 2·5; G, detail of B, × 2·8; H, detail of latex cast of B, × 3·4. I, exterior of incomplete dorsal valve, Skålberget, SMNH Br102556*a*, × 2·5.

T. rugosa is comparatively large for the family, the maximum width being almost 27 mm. Most other elkaniids (such as *Broeggeria*, *Elkania*, *and Elkanisca*) are generally up to 10 mm wide; only *Monobolina crassa* (maximum width 23 mm) and '*Aulonotreta*' *kuraganica* (maximum width 25 mm) are more than 20 mm wide. Cooper (1956, p. 193, pl. 9F: 16, 11A: 1) described a large, unnamed obolid, *Obolus*? sp. 3, from the Middle Ordovician Pratt Ferry beds of Alabama, USA. The interior of this species is unknown, but the strongly rugose exterior, and the general shape of the shell indicate that it might possibly be related to *Tilasia*.

As noted above, *T. rugosa* is the youngest described elkaniid and the first record of the family from the Upper Ordovician (Harju Series).

Remarks on autecology. The type of environment in which *T. rugosa* lived is uncertain. The holotype is a complete, articulated shell, which has probably not been transported for any great distance after death, but its exact location within the carbonate mound is not known. The mound core of the Boda Limestone is generally poor in sedentary macro-organisms, and has dominantly a vagile fauna of trilobites, gastropods, cephalopods, and pelecypods (Jaanusson 1982, p. 28). Two dorsal valves, which were collected from the flank facies of the mound, are fragmentary and may have been transported.

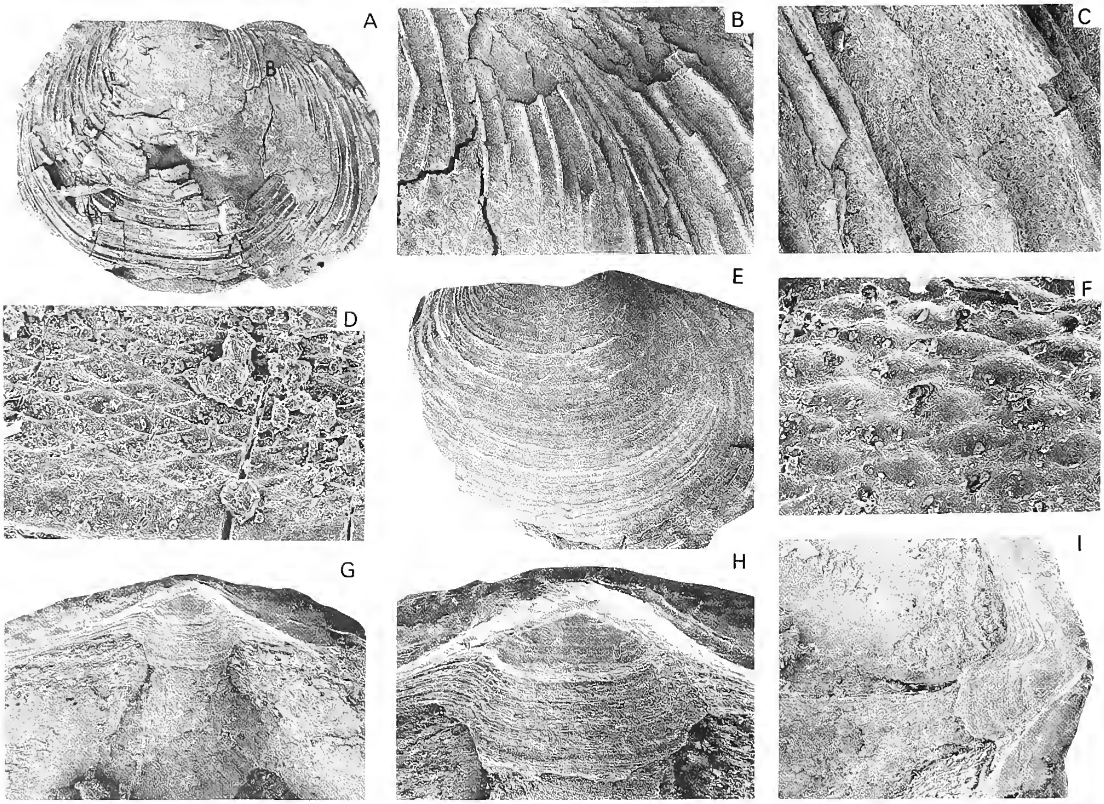
Although many fossil lingulaceans appear to have been infaunal burrowers comparable with their Recent representatives, this is an unlikely mode of life for *T. rugosa*. The following characters makes it comparatively poorly adapted for burrowing (see Bassett 1984 and Savazzi 1986 for a detailed discussion of this life strategy): (1) The moderately biconvex shell is transversely suboval and wider than long (rather than elongate and 'streamlined' as in *Lingula*). (2) The visceral area and the sites of muscular attachments are more posteriorly placed as compared with other lingulaceans (the dorsal anterior lateral muscle scars are placed at about 40% the valve length from the posterior margin in *T. rugosa*, whereas in *Lingula*, for example, the ratio is about 60–70%). (3) The ornamentation is strongly rugose (rather than smooth, or with burrowing sculptures). Thus, *T. rugosa* was probably better adapted to some kind of epifaunal mode of life. The pedicle foramen appears to have remained open throughout ontogeny.

Occurrence. T. rugosa is restricted to the Ashgill Boda Limestone of Dalarna.

MICRO-ORNAMENTATION

Under the SEM, the etched rugose exterior of two dorsal valves revealed a regular pattern of pits covering the post-larval surface (Text-fig. 4A–F). The apical region of the valves is fragmentary, and the ornamentation is not known from this part of the shell.

The pits are evenly distributed and closely packed, less than 10 μm deep, subequal in size and shape, elongate rhomboid, up to 100 μm long and 30 μm wide, with the largest dimension arranged



TEXT-FIG. 4. *Tilasia rugosa* sp. nov., Boda Limestone (Ashgill), Siljan district, Dalarna. A, exterior of incomplete dorsal valve, the location of B indicated, Skålberget, SMNH Br133691, × 5. B, C, D, details of A, × 19, × 60, × 150, respectively. E, exterior of partly exfoliated, incomplete dorsal valve (see also Text-fig. 3I), Skålberget, SMNH Br102556*a*, × 5. F, detail of E, × 196. G, interior of incomplete ventral valve, Östbjörka, LO 5956, × 10. H, detail of G, × 20. I, oblique lateral view of G, × 15.

perpendicular to the direction of growth (Text-fig. 4C). The geometry of the ornamentation could not be investigated in detail, owing to the considerable degree of fragmentation and exfoliation in the two available valves. However, the pits appear to be arranged in offset radiating rows (*sensu* Wright 1981, p. 446). Each rhomboid pit is defined by two pairs of parallel ridges (each up to 5 μm wide), which are disposed obliquely across the valve surface and intersect at about 30–40°. This type of sculpture is very suggestive of the so-called divaricate pattern of ornamentation, which is responsible for a wide range of sculptures (including burrowing terraces) in molluscs and arthropods, but it has also been reported from some lingulacean brachiopods (see Seilacher 1972 and Savazzi 1986 for reviews).

A divaricate ornamentation of pits has not previously been reported from the elkaniids, but the Lower Ordovician species *Dictyobolus* [= ?*Lamanskya*] *transversus* Williams and Curry (1985, p. 189, figs 2–7) and *Lamanskya splendens* Moberg and Segerberg have an essentially identical type of ornamentation; a similar type of sculpture also appears to be developed in '*Aulonotreta*' *kuraganica* Andreeva. As noted above, these taxa are here considered to belong within the family (Holmer, unpublished).

Ornamentation comparable to that of the elkaniids is also known from three other brachiopod groups: (1) The problematic articulate brachiopod *Dictyonella* has rhomboid pits, very similar to those of *Tilasia* and arranged in a strict divaricate geometry (see Wright 1981 for a detailed discussion); however, this brachiopod is not otherwise comparable with the elkaniids. (2) Rhomboid, post-larval pits, only some 6 μm across, and arranged in divaricate rows have been described by Popov *et al.* (1982, fig. 1: 2) and Holmer (1986, fig. 40) from the thin-shelled Ordovician lingulacean *Paterula*. In the paterulids, the larval shell is also pitted, with minute, circular, cross-cutting pits, about 2–4 μm across, which are closely comparable with the larval pits of most acrotretaceans (see Biernat and Williams 1970). Popov *et al.* (1982, p. 103) suggested that both the larval and post-larval pits of *Paterula* represent moulds of a vesicular periostracum, as in the 'bubble raft' model originally proposed for the acrotretacean larval shell (Biernat and Williams 1970). It is entirely possible that the post-larval pits of *Tilasia* represent a cast of similar structures in the periostracum (see also Williams 1990). (3) Most paterinids (like *Dictyonina* and *Micromitra*) appear to have divaricate types of post-larval pitted ornamentation, whereas the larval shell is smooth (e.g. Rowell 1965); in *Dictyonites* and *Lacunites*, there are rounded, open perforations, 20–200 μm across, which penetrate the valves (Cooper 1956; Wright 1981; Holmer 1986, 1989), and the problematic phosphatic brachiopod *Volborthia* (sometimes doubtfully referred to the paterinids) possesses some kind of pitted, divaricate ornamentation, which has not been studied closely (Ushatinskaya *et al.* 1988, pl. 6: 6*a*).

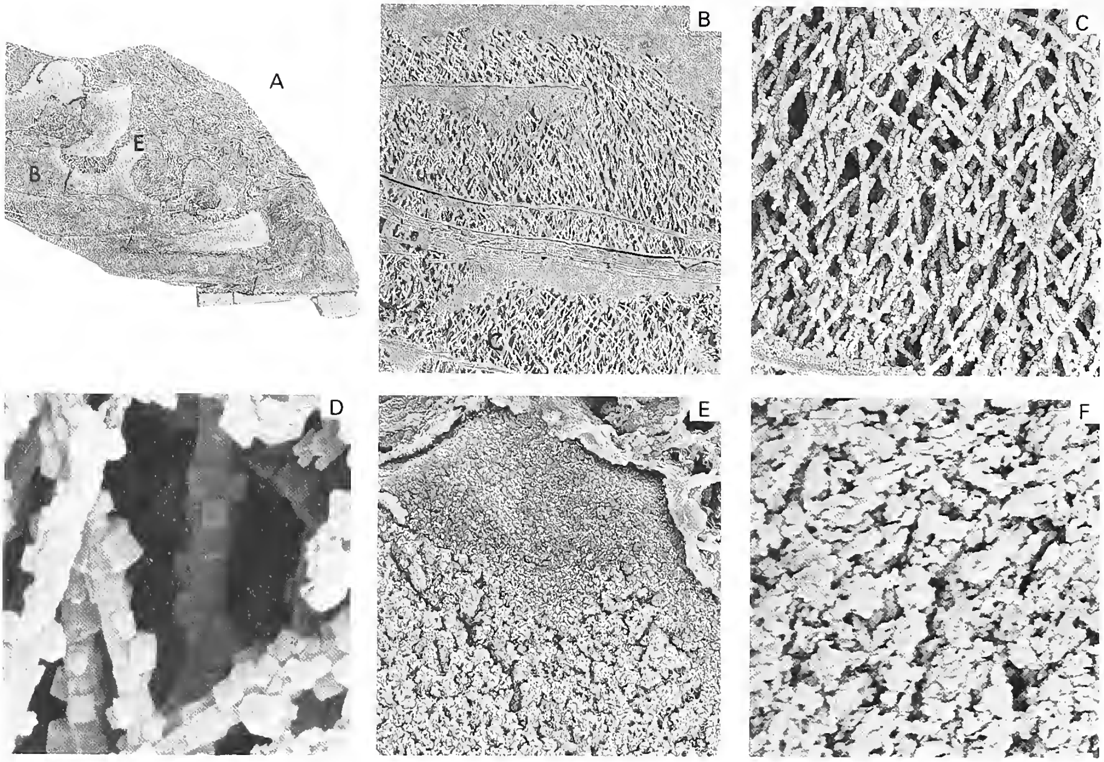
Other types of pitted post-larval ornamentation have been reported and discussed by Wreight (1981), Savazzi (1986), and Holmer (1986, 1987, 1989).

SHELL STRUCTURE

Because of the limited material available, only a single fragment of the postero-lateral portion of a dorsal valve was sectioned (Text-fig. 5). The rugose exterior of this fragment is still covered by the calcareous matrix of the Boda Limestone (Text-fig. 5A).

The pitted ornamentation, described above, is developed in the outermost primary layer, which is only about 10 μm thick (Text-fig. 5E). In etched sections examined under the SEM, it has a densely granular appearance, but the size of individual apatite granulae could not be determined, and the layer appears to lack birefringence. The boundary to the secondary layer is not well defined (Text-fig. 5E), and the primary layer is not easily 'peeled off' as in some discinaceans (Holmer 1987).

The secondary layer is primarily built up of laminae, up to 0·3 mm thick, which are roughly wedge-shaped in section, and inclined at a low angle to the outer valve surface. The laminae have a porous appearance both under the SEM and the light microscope, and possess a well-developed baculate structure (*sensu* Holmer 1989), with criss-crossing slender apatite baculae, about 1–2 μm across (Text-fig. 5B, C). The detailed internal structure of the baculae could not be determined; they



TEXT-FIG. 5. A, Polished and etched section through a fragment of a dorsal valve of *Tilasia rugosa* sp. nov., the location of B and E indicated, Boda Limestone (Ashgill), Skålberget, Siljan district, Dalarna, SMNH Br102556*c*, × 27. B, detail of A, the location of C is indicated, × 180. C, detail of B, × 750. D, detail of C, × 2250. E, detail of A, × 1660. F, detail of E, × 5900.

are covered by numerous minute apatite granulae, which sometimes are cube-shaped, up to 0·5 μm across (Text-fig. 5D); these structures are possibly related to secondary cyrstal growth during diagenesis.

In the inner part of each lamina the interbacular spaces are empty, which causes the baculae to stand out in relief in etched sections; on the outer zone, directly beneath the primary layer, these spaces appear to be filled by a granular apatite matrix (Text-fig. 5B–D, F). The thick baculate laminae are separated by thin, homogenous lamellae, consisting of minutely granular apatite (Text-fig. 5B). The apatite of the secondary layer is strongly birefringent, and the main preferred orientation of the *c*-axes appears to be roughly normal, or at a high angle to the laminae; only in some of the thin granular lamellae are there indications of a different preferred *c*-axis orientation, parallel relative to the lamellae.

The shell structure of *Tilasia* is nearly indentical to that of other Lower Palaeozoic lingulaceans discussed by Holmer (1989). The shell structure of most Lower Palaeozoic lingulaceans can be interpreted in the light of what is now known about Recent *Glottidia*, which has a well-defined primary layer and a baculate structure penetrating the organic laminae of the secondary layer (see Iwata 1982; Watabe and Pan 1984; Pan and Watabe 1988 for details).

Holmer (1987) and Ushatinskaya *et al.* (1988) noted that the shell structure of fossil discinaceans is comparable with that of the lingulaceans, and that they can also be compared with their Recent representatives (see Iwata 1982).

Ushatinskaya *et al.* (1988, p. 49; see also Hewitt 1980; Popov and Ushatinskaya 1986;

Ushatinskaya and Zezina 1988) suggested that the shell structures present in both the fossil and Recent phosphatic brachiopods could have been formed by a complete *post-mortem* redistribution of phosphate, and phosphatization of the organic matter in the shell. One of the main reasons for this proposal seems to be that phosphatic, rod-like strutures, somewhat similar to the brachiopod baculae, have been described by Hewitt and Stait (1985) from the phosphatized connecting rings of some Ordovician cephalopods.

There are two kinds of rod-like structures present in the cephalopod connecting rings; the first type apparently represent secondarily phosphatized spicules, originally consisting of aragonite (Hewitt and Stait 1985, figs 5 and 7), whereas the second type is formed by 'dendritic granular crystals on the interior of the connecting ring' (Hewitt and Stait 1985, fig. 2). For obvious reasons, the phosphatized aragonite spicules are most unlikely to be comparable with the baculae described from lingulacean and discinacean brachiopods. The second irregular, dendritic pattern of granular apatite 'rods' appears to have grown in contact with the surface represented by the connecting ring, rather than representing isolated criss-crossing rods as in the lingulacean baculae. Moreover, the sections of Recent *Glottidia*, examined by Iwata (1982), Watabe and Pan (1984), and Pan and Watabe (1988) were prepared using freshly killed specimens; it is highly unlikely that a complete redistribution of phosphate could have occurred in these specimens as was suggested by Ushatinskaya *et al.* (1988).

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CUTICULAR ULTRASTRUCTURE OF THE TRILOBITE *ELLIPSOCEPHALUS POLYTOMUS* FROM THE MIDDLE CAMBRIAN OF ÖLAND, SWEDEN

by J. E. DALINGWATER, S. J. HUTCHINSON, H. MUTVEI *and* D. J. SIVETER

ABSTRACT. Hand specimens and polished sections of the cuticle of the trilobite *Ellipsocephalus polytomus* Linnarsson from the Middle Cambrian of Öland, Sweden have been examined in incident light and, after etching, with the scanning electron microscope. A thin (25–50 μm) outer layer comprises about twenty lamina units; the structure of these units is interpreted as representing the original inorganic material of the cuticle, and therefore also reflecting the structure of the original organic template. X-ray microanalysis strongly suggests that this outer layer is now composed of calcium phosphate. Cavities, 15 μm in diameter, in the outer layer connect to 3 μm diameter canals which extend across the principal layer of the cuticle: these resemble the gland ducts of a Recent millipede. Pore canal pathways may be represented by elongate openings on the undersurface of the outer layer, and structures resembling the interprismatic septa of Recent decapod crustaceans are seen in angled slices. Other primary microstructures identified are relict organic material and fibres which may have bound together the major layers of the cuticle. Horizontal tubules on the undersurface of the outer layer are possibly infilled borings of cyanobacteria.

Major subdivisions of *Ellipsocephalus* cuticle in life are proposed as: a very thin outermost epicuticle, an outer laminated layer, and a principal layer, the original structure of which is represented only by disc-like extensions on the perpendicular canals which pass across it.

TRILOBITE cuticular microstructure has been extensively investigated over the past twenty years (see Dalingwater 1973; Teigler and Towe 1975; Dalingwater and Miller 1977, Størmer 1980; Wilmot and Fallick 1989; Wilmot 1990*a*), yet our knowledge of the overall structure of the cuticle is far from complete, and the only detailed information on ultrastructure of lamina units has been provided by Mutvei (1981) from a *Flexicalymene* species from the upper Ordovician of Iowa.

In this paper we describe ultrastructural detail from an outer cuticular layer of the Middle Cambrian trilobite *Ellipsocephalus polytomus* Linnarsson, 1877, from Enerum, Öland, Sweden, which is superior to anything previously reported from any trilobite cuticle. We analyze our observations in relation to Recent arthropod material, assess the implications for views on the overall structure of the trilobite cuticle and outline areas for further investigation.

MATERIALS AND METHODS

The collections of the Naturhistoriska Riksmuseet in Stockholm contain specimens of the Middle Cambrian trilobite genus *Ellipsocephalus* preserved in different lithologies: shales, limestones and even conglomerates. However, the best-preserved material seems to be in the Middle Cambrian glauconitic limestones from Enerum and Borgholm on the Baltic island of Öland. Specimens of *Ellipsocephalus polytomus* from these localities are almost exclusively cranidia, although the collections also include a few complete dorsal exoskeletons. A series of pieces of glauconitic limestone containing cranidia of *Ellipsocephalus polytomus* and *Paradoxides* sp. fragments collected by Westergård from 'a boulder at Enerum, Öland in 1930' were selected for study.

The surface of the cuticle of *Ellipsocephalus* was examined and photographed in incident light.

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Slices of the limestone, approximately 2 mm thick, were cut away from blocks of material with a thin high-speed diamond wheel, after one face had been flattened on rotating wheels covered with carborundum-impregnated papers and lubricated with water, and polished to a mirror finish using ultra-fine diamond pastes on felt buffing wheels. Material prepared in this way was examined under a stereo binocular microscope in incident light. Further slices prepared in a similar fashion were etched in a supersaturated aqueous solution of ethylenediaminotetracetic acid (disodium salt) for up to three hours, with the etching process observed from time to time under a stereo binocular microscope in incident light. Etched slices were carefully washed in de-ionised water, air dried, gold sputter-coated and examined with a Cambridge S360 scanning electron microscope (SEM) under optimum conditions for high resolution (short working distance, high accelerating voltage, small aperture size, small spot size). In all, eleven etched preparations were made for SEM examination; each preparation contained at least two and as many as five sections of *Ellipsocephalus* cuticle, as well as those of *Paradoxides* sp. Most of the slices were deliberately cut in such a way that the cuticle was sectioned more or less perpendicular to the cuticle surface, though a few angled slices were accidentally produced and a few deliberately achieved. In addition, an accidental but fortuitous break of cuticle along a low angle from the horizontal was made; part and counterpart of this break were examined unetched with the SEM.

Two further preparations were carbon coated and analysed with the LINK system of X-ray microanalysis attached to a Cambridge S360 SEM.

All preparations are stored with their parent specimens (Ar 46218*a*–*f*) in the Sektionen för Paleozoologi, Naturhistoriska Riksmuseet, Stockholm (RM).

DESCRIPTION OF THE CUTICLE

Terminology

We follow Dennell's (1973) terminology for horizontal laminations of the cuticle: each *lamina unit* is considered to consist of a narrower *lamina* and a wider *inter-lamina*. This contrasts with the view of Bouligand (1965) who considered the lamination of arthropod cuticles as an artefact resulting from the sectioning of horizontal sheets of fibres with fibre orientation changing from one sheet to the next. (For a more detailed discussion see Dalingwater and Mutvei 1990).

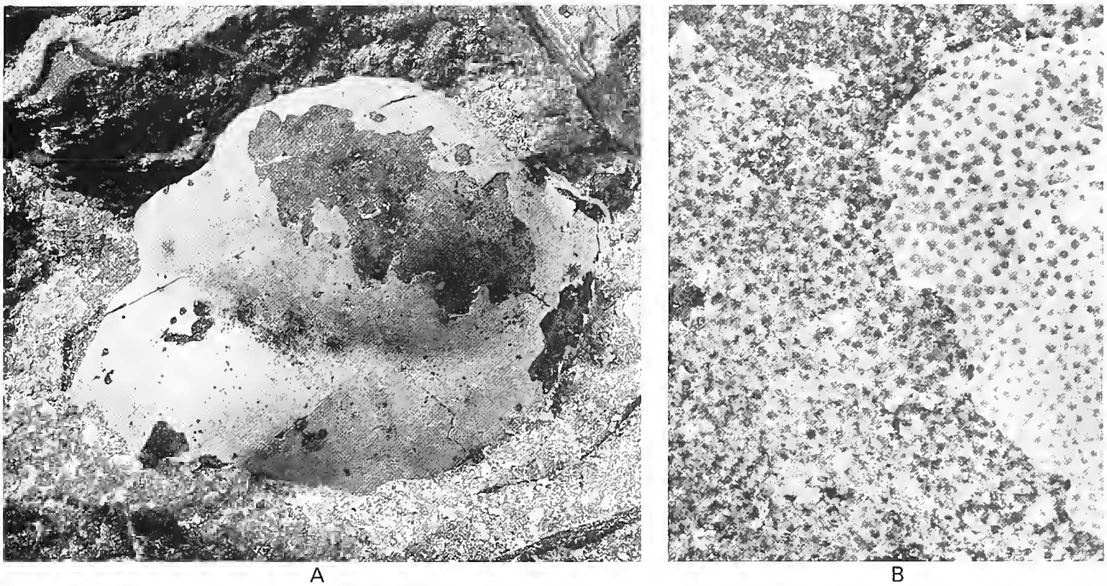
Hand specimens

A consistent feature of *Ellipsocephalus* specimens from Öland is a thin outer layer which has a faint pinkish tinge: this was commented on by Teigler and Towe (1975, pp. 138–139) who also established that a similar thin outer layer in a Silurian calymenid from Poland was composed of calcium phosphate, probably in the form of apatite.

Specimens of *Paradoxides* sp., in the same beds on Öland do not have a thin layer of this nature. The layer does not completely cover all parts of every *Ellipsocephalus* specimen: it is often worn away from the prominence of the glabella (Text-fig 1A) and, in a few examples, seems to be absent, possibly removed on the counterpart. In the latter situation, the brown exposed 'surface' of the cuticle has the shiny appearance characteristic of other well-preserved trilobites. It is possible to find two *Ellipsocephalus* cranidia side by side on the same bedding plane, one with a pinkish outer layer, the other apparently without. However, when examined under a microscope, at least traces of the outer layer can be found on all specimens. In the very rare 'complete' specimens of *Ellipsocephalus*, all parts of the dorsal exoskeleton are seen to be covered by the outer layer.

Hand specimens and polished slices viewed in incident light

When the surface of the outer layer is viewed in incident light at low magnifications, almost its entire area appears to be patterned with small circular punctations, about 15 μm in diameter (Text-fig. 1B). The spacing of these punctations is somewhat irregular: in places they are almost contiguous, contrasting with small clear patches, but on average they are 15 μm apart. In areas where the outer



TEXT-FIG. 1. *Ellipsocephalus polytomus* Linnarsson from Enerum, Öland, Sweden. Specimen RM Ar 46218*c*. A, cranidium, × 5. B, detail of surface punctations, × 100.

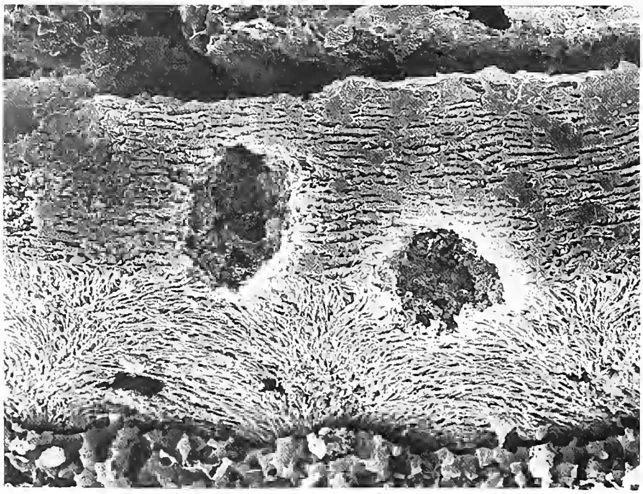
layer has been worn away or removed on the counterpart, the punctations can still clearly be seen, and also some light circular areas about 40 μm in diameter each perforated by a minute (*c.* 1 μm) opening. These light circles are about 200 μm apart: a similar spacing to that of the patches devoid of punctations on the outer layer surface.

In polished slices, sections of *Ellipsocephalus* cuticle can easily be identified by their shape and by the possession of a thin whitish outer layer, which at higher magnifications is seen to contain darker spherulitic structures around 15 μm in diameter. The region of cuticle below the outer layer is dark brown and penetrated by numerous fine perpendicular canals which stand out as they are paler than the ground material of the inner layer.

SEM preparations

General structure of the cuticle. The great predominance of cranidia on the surface of the hand specimens led us to assume that the great majority, if not all, of the *Ellipsocephalus* material was of sections of that part of the cephalon. As in material examined with the light microscope, the shape of many of the sections reinforced the validity of this conclusion.

The etching process left a thin outer layer, 25–50 μm thick, standing clear and unaltered from the rest of the cuticle, up to 200 μm thick, which was etched inwards. Not only could the outer layer be viewed in perpendicular section, but its inner undersurface could also be examined, for example in preparation RM Ar 46218*b*-E4 (Text-fig. 2). In that particular preparation, the perpendicular face clearly shows that the outer layer comprises about twenty lamina units, each just over 1 μm thick. The majority of preparations show a similar aspect to that of E4, but a few are different, possibly the result of: (i) slight differences in preparation technique, including direction of sectioning and quality of polishing; (ii) original differences in the cuticles, possibly including those related to the size of the animal; (iii) localized diagenetic differences. In preparation RM Ar 46218*e*-E9 (Pl. 1, fig. 1), the outer layer is somewhat thicker (nearly 50 μm thick) than in most other preparations and the lamination is very clearly defined. There are about thirty-five lamina units, each nearly 1·5 μm thick except for the outer five units which are thinner. In areas of a few preparations, for



TEXT-FIG. 2. Scanning electron micrograph of etched perpendicular section of *Ellipsocephalus polytomus* Linnarsson cuticle outer layer, also with a view of undersurface of that layer. Preparation RM Ar 46218*b*-E4, ×800.

example RM Ar 46218*b*-E1 (Pl. 1, fig. 2), the lamination is less clear and transforms laterally into a zone of semi-prismatic calcite crystallites, and in one preparation, RM Ar 46218*b*-Ei (Pl. 1, fig. 3), the lamination is penetrated by calcite crystallites. Preparations RM Ar 46218*b*-E1 and -Ei are both perpendicular sections (deduced from the perpendicular pathways of their canals) and so this transformation or penetration is a real phenomenon and not an artefact produced by angled sectioning.

In many sections round or elliptical cavities, up to 15μm in diameter and up to 20 μm high, extend from the lower edge of the outer layer to near the surface of the cuticle. However, they never reach beyond the uppermost fine lamina units, nor was any connection between these cavities and the cuticle surface observed in any of the sections examined.

Another feature in many sections is an outermost non-laminate region of cuticle, up to 2 μm thick and with a dense homogenous appearance. This can be seen most clearly in Plate 1, figure 1 and Plate 3, figure 4.

The main region of the cuticle (for convenience termed the principal layer) consists of fine crystallites, presumably of calcite, sometimes with their long axes arranged roughly perpendicular to the cuticle surface. This region shows little detail apart from this feature, but is penetrated by perpendicular canals, approximately 3 μm in diameter (Pl. 1, fig. 4). These canals have disc-like lateral extensions about 0·5 μm thick and on average the same distance apart (Pl. 1, fig. 5). Preparations in which the principal layer is etched deeply inwards illustrate how numerous and ubiquitous these canals are (Pl. 1, fig. 6).

Lamina unit ultrastructure. At higher magnifications, considerable ultrastructural detail can be resolved. At first, a bewildering array of apparently different structures was observed. But eventually, by always taking micrographs at a standard series of screen magnifications, it became clear that at least some of the apparent variation was the result of viewing essentially similar

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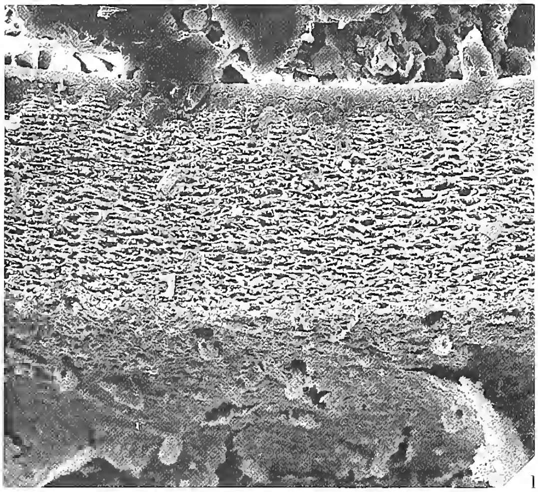
EXPLANATION OF PLATE 1

Figs 1–6. *Ellipsocephalus polytomus* Linnarsson, Middle Cambrian, Enerum, Öland, Sweden. Scanning electron micrographs of etched sections of cranidial cuticle. 1–3, outer laminated layer in preparations RM Ar 46218*e*-E9, *b*-E1, *b*-Ei, respectively, all ×650. 4–6, perpendicular canals in the principal layer in preparations RM Ar 46218*b*-E5, ×300, *b*-E5, ×8000, *e*-E9 ×250, respectively.

PLATE 1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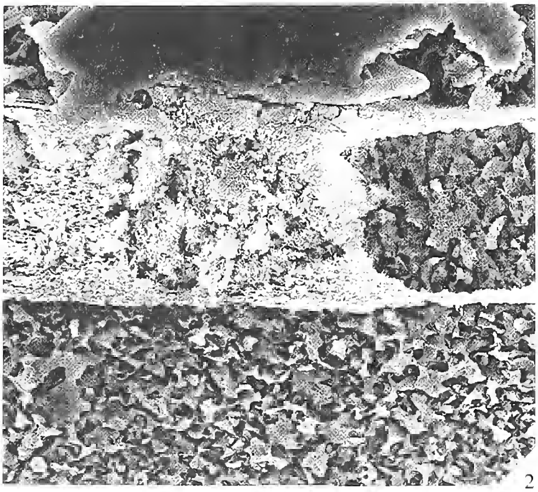
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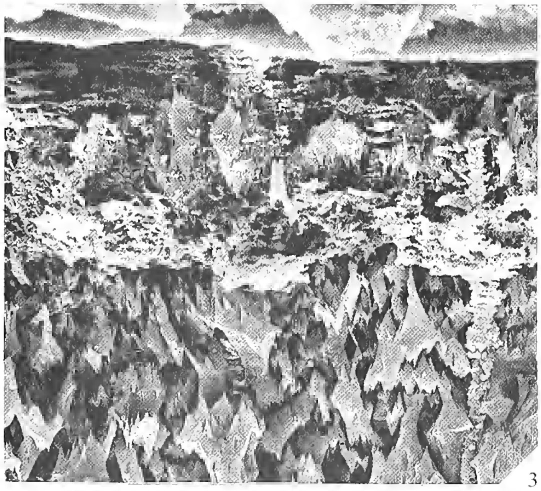
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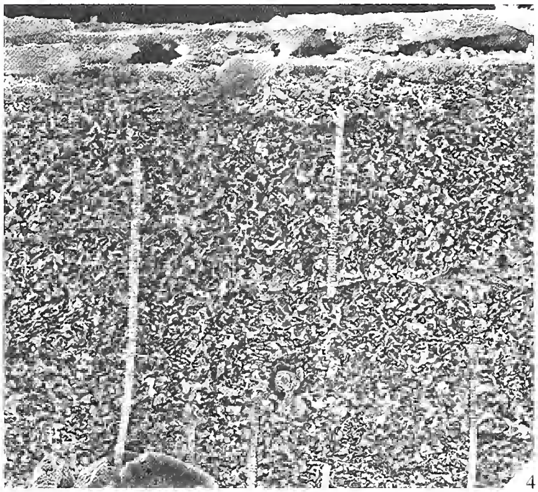
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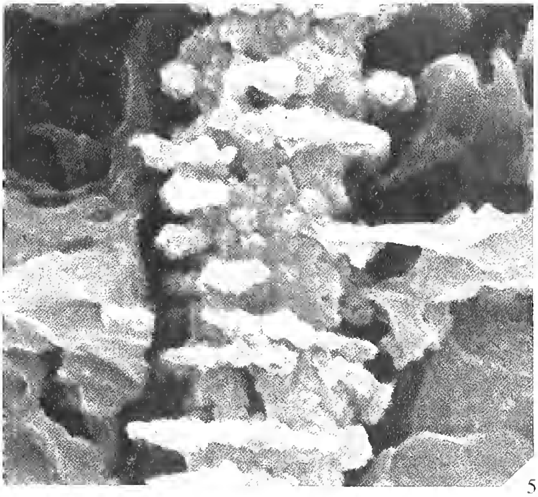
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structures at arbitrary magnifications, with slight differences in preparation method, angle of slicing and angle of viewing also contributing to variability. Plate 2, figure 1 shows lamina units with their sectional edges flattened by the polishing procedure, whereas those in Plate 2, figure 2 show a more broken appearance. The interface between the perpendicular face and the horizontal undersurface of the outer layer was also examined (Pl. 2, fig. 3). In all three micrographs the laminae appear to be composed of arrays of rods, with more or less circular cross-sections, linked together in sheets; some sheets seem to arc across the inter-laminae. A detailed view of the undersurface of the outer layer (Pl. 2, fig. 4) shows that the fingerprint-like patterns seen in Text-figure 2 are produced by arced sheets of fibrous material. A near-horizontal view of a lamina unit in an unetched break (Pl. 2, fig. 5) reveals a herringbone-like pattern of rods. In contrast, a near-horizontal slice, despite being subjected to flattening and polishing (or perhaps because of this) shows a mosaic of fibrous and rod-like material from different levels of the cuticle (Pl. 2, fig. 6, which is a detail of Pl. 3, fig. 5).

Polygonal patterns. In sub-surface areas of the unetched preparation viewed from above, polygonal areas about 40 μm across and delimited by slightly raised ridges can be detected (Pl. 3, fig. 1).

Cavities. Round or elliptical cavities have already been mentioned as a consistent feature of the outer layer of cuticle. At low magnifications, arrays of these cavities can be seen, with the broken upper portions of perpendicular canals below them (Pl. 3, fig. 4). In preparations sliced at an angle of a few degrees from the horizontal, the outer layer is perhaps somewhat disrupted by the effect of the etching process on the principal layer; the latter can be seen through the cavities (Pl. 3, fig. 5). One preparation in which the principal layer has been etched inwards to a considerable extent, leaving the outer layer roofing a miniature cave (Pl. 3, fig. 6), shows the stumps of canals as stalactic projections from the cave roof, clearly connecting to the cavities in the outer layer which are 'illuminated' by the electron beam striking the top surface of the cuticle and 'shining through it'. On the right of the micrograph, a rather stouter perpendicular canal is the only one left extending from the inner matrix to the outer layer.

Other structures. The undersurface of the outer layer in some preparations seems to be covered by a thin coating skin through which some details of that undersurface can still be seen. This skin often peels back or breaks open to reveal clearer details. This phenomenon can just be seen on the bottom right of Plate 1, figure 1. Roughly star-shaped arrays of fibrous or crystalline material (Pl. 3, fig. 2) stand out below the general level of the undersurface of the outer layer in some preparations. In some areas of nearly all preparations, horizontal tubular structures 1–2 μm in diameter criss-cross the undersurface of the outer layer, sometimes forming node-like structures where they intersect (Pl. 3, fig. 3).

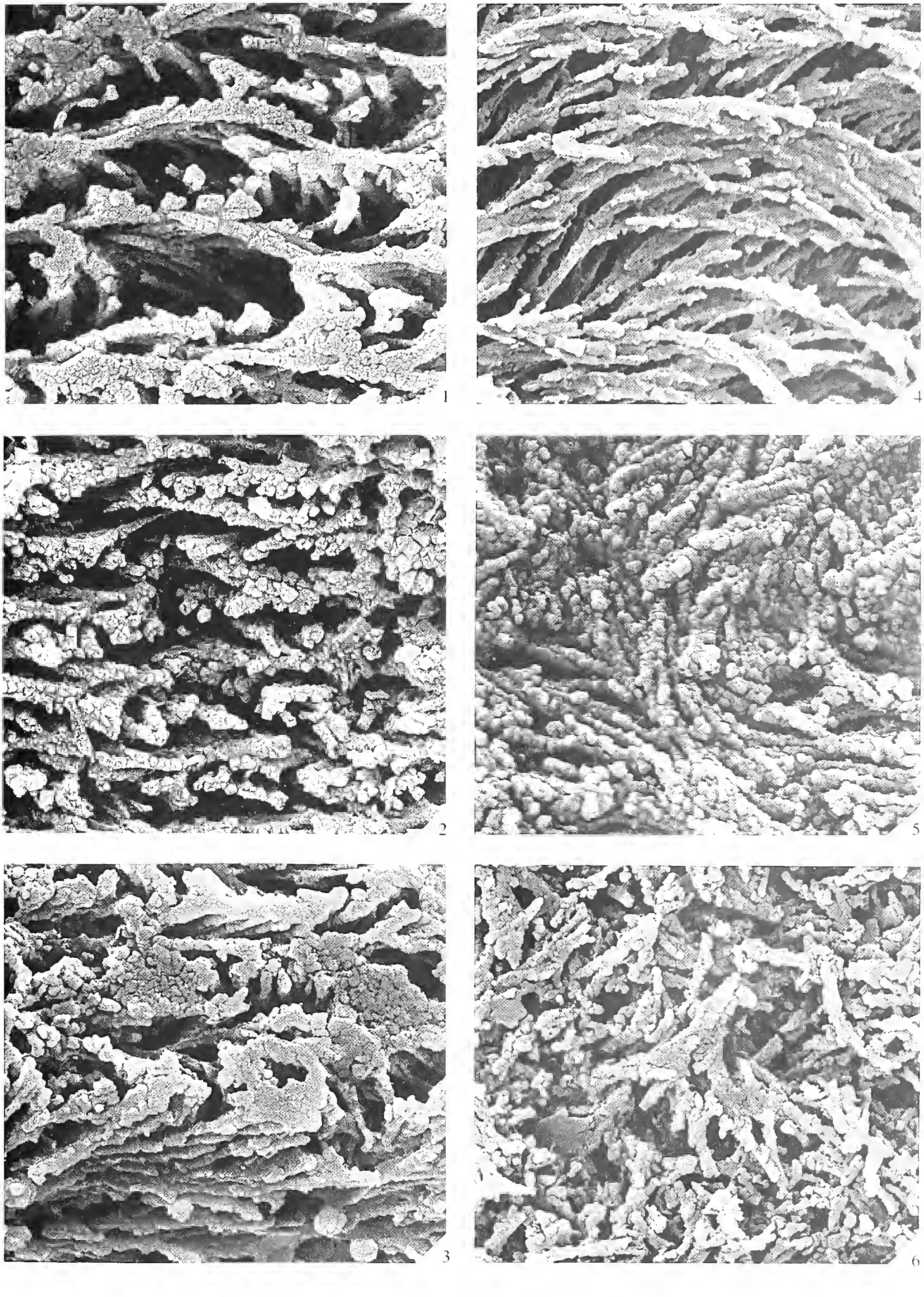
COMPOSITION

Semi-quantitative elemental analysis, using the LINK system of X-ray microanalysis attached to the SEM gave peaks for calcium and phosphorus in the outer layer, whereas the principal layer showed a strong peak only for calcium with lesser peaks for silicon and iron and only a trace of phosphorus.

EXPLANATION OF PLATE 2

Figs 1–6. *Ellipsocephalus polytomus* Linnarsson, Middle Cambrian, Enerum, Öland, Sweden. Scanning electron micrographs of etched sections (except 5) of cranidial cuticle showing details of outer layer, all ×9000. 1 and 2, lamina units in preparations RM Ar 46218*e*-E9, *b*-E4. 3, interface between vertical section and undersurface, preparation RM Ar 46218*b*-E4. 4, undersurface, preparation RM Ar 46218*b*-E4. 5, unetched low angle break, preparation RM Ar 46218*e*-E8. 6, low angle slice, preparation RM Ar 46218*b*-E6.

PLATE 2



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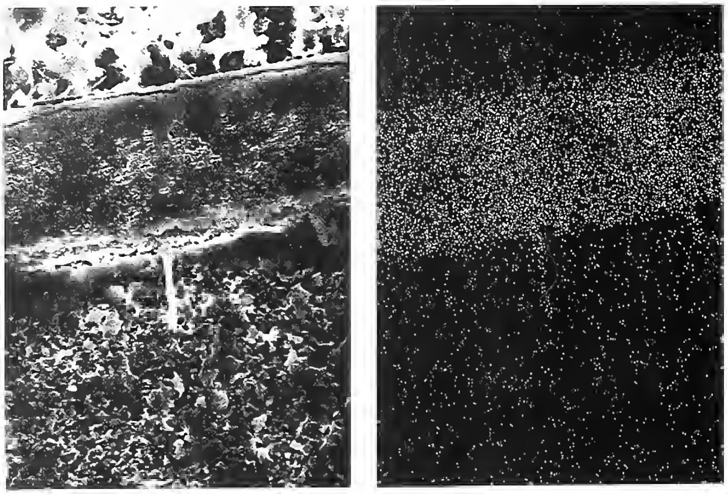

TEXT-FIG. 3. Etched perpendicular section of *Ellipsocephalus polytomus* Linnarsson cuticle outer layer. Left, scanning electron micrograph; right, spot X-ray microanalysis for phosphorus. Preparation RM Ar 46218-A2, × 450.

A spot analysis for phosphorus showed an exact co-incidence of the concentration of phosphorus with the outer layer (Text-fig. 3) and also suggested that the 3 μm perpendicular canals contain high concentrations of phosphorus.

DISCUSSION

Subdivisions of trilobite cuticle

Stormer (1980) discussed the broad divisions of the trilobite cuticle and generally supported Dalingwater and Miller's (1977) view that it consisted of an outer prismatic layer and a principal layer with three distinct laminate zones – an outer zone with narrow lamina units, a middle zone with a few relatively wide units and an inner zone with a few narrow units. Størmer also recognized that rarely are all regions of the cuticle equally well represented or well preserved in any one example. Teigler and Towe (1975) have argued for two basic layers of cuticle, suggesting that the thin outer layer may be prismatic or pigmented or apatitic.

Our interpretation of *Ellipsocephalus* cuticle is that in life the outer laminated layer had only the thin apparently structureless outermost layer above it, the latter possibly representing an epicuticle. Furthermore, the lateral transition between laminated cuticle and prismatic cuticle in one preparation and the invasion of the laminated layer by calcite crystallites in another suggests that the prismatic layer observed in the cuticle of many trilobites may not be an original layer. However, much more evidence is needed before we can firmly draw this conclusion.

Ultrastructural detail of lamina units

Calcified cuticles of Recent arthropods, for example those of decapod crustaceans, have organic

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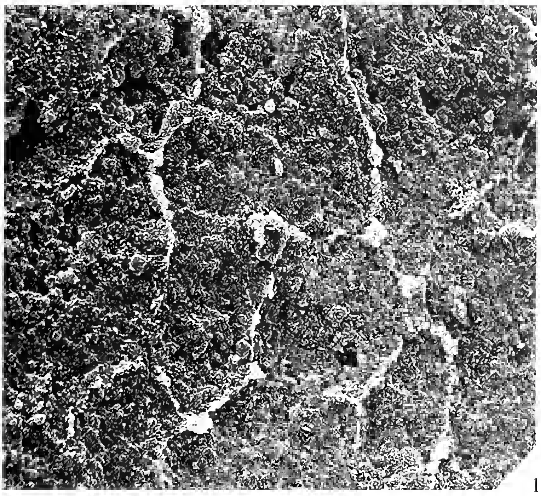
EXPLANATION OF PLATE 3

Figs 1–6. *Ellipsocephalus polytomus* Linnarsson, Middle Cambrian, Enerum, Öland, Sweden. Scanning electron micrographs of etched sections (except 1) of cranidial cuticle. 1, low angle break, showing prismatic structures, preparation RM Ar 46218*e*-E8, × 500. 2, arrays of fibrous material on outer layer undersurface, preparation RM Ar 46218*b*-E4, × 9000. 3, tubular structures on undersurface of outer layer, preparation RM Ar 46218*e*-E9, × 1200. 4–6, cavities in the outer layer; 4, perpendicular sectional view, preparation RM Ar 46218*b*-Ei, × 300; 5, from above, preparation RMAr 46218*b*-E4, × 1000; 6, from slightly below, 'illuminated' by beam striking top surface, preparation RM Ar 46218*e*-E9, × 300.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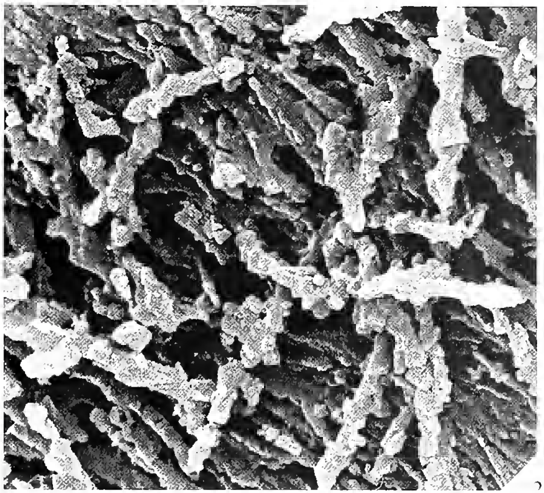
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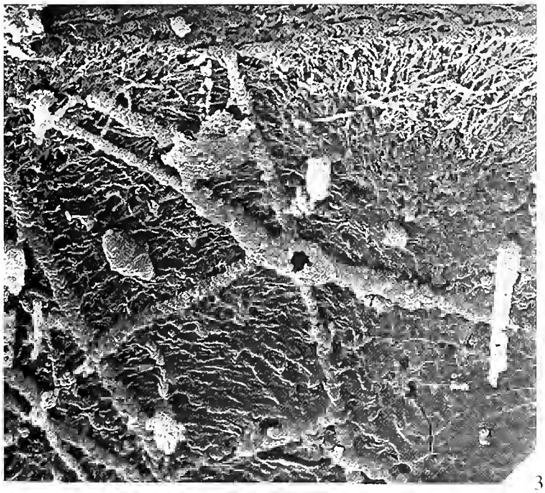
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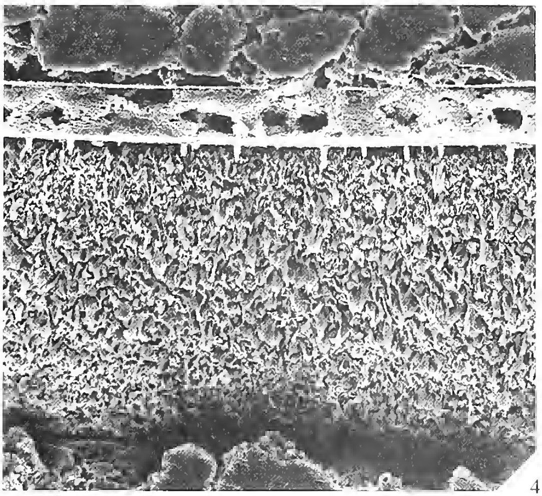
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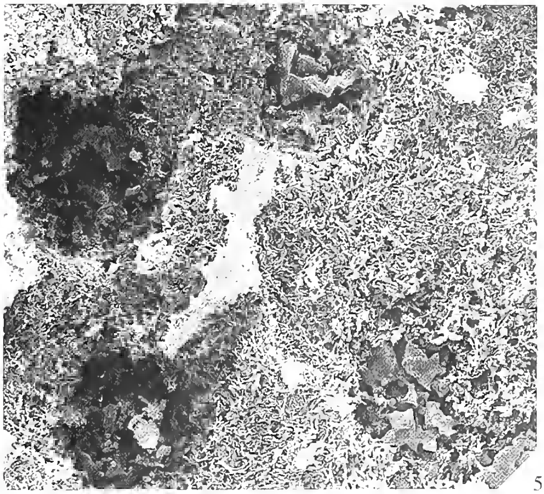
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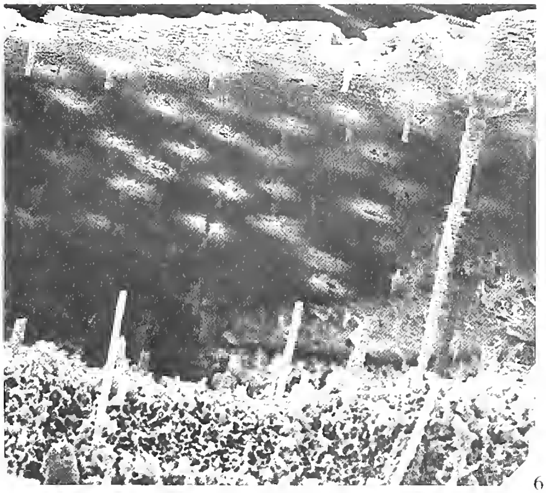
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templates upon or within which inorganic salts are deposited. On analysis, these templates show at least three levels of structural organization (Giraud-Guille 1984*a*). Near-molecular associations of chitin and proteins to form microfibrils represent the first level; associations of microfibrils in reticulate, macrofibrillar or homogenous arrays form the second level; and spatial arrangements of level two associations (e.g. macrofibrils in helicoidal arrays) give the third level. Minerals are probably deposited within the reticulate arrangement of microfibrils in the decapod crustacean exocuticle and around the macrofibres of the calcified zone; homogenous arrays of microfibrils effectively fill all available space in the uncalcified endocuticle. It is quite possible to envisage the three-dimensional arrangement both of organic template and deposited minerals in the decapod crustacean calcified zone if one accepts the Bouligand–Neville interpretation of laminated cuticles. In fact, the model was originally proposed after examination of *Carcinus* calcified zone macrofibrils (Bouligand 1965), but later shown to be more widely applicable to microfibrillar arrangements, for example in insect cuticles (Neville 1975).

It is, however, at the third level of cuticular architectural organization that the Dennell–Mutvei–Dalingwater view (see Dalingwater and Mutvei 1990 for a more detailed discussion) does not accord with the Bouligand–Neville model: the former suggest that laminae are real structures and that sheets of fibres arc across the inter-laminae. In this context it is interesting to note that it is difficult to produce a satisfactory three-dimensional helicoidal arrangement for the reticulate associations of exocuticular microfibrils: Giraud-Guille (1984*a*, p. 81, fig. 6) has illustrated a semi-helicoidal pattern with fibre direction changing in blocks, but even that is not easily reconciled with the reality of her excellent micrographs.

In Recent decapod crustacean material examined with the SEM, it is difficult to distinguish between organic template and deposited minerals, even with the help of transmission electron micrographs of the same material in which all inorganic material has been removed by decalcification prior to sectioning. So interpretation of lamina unit ultrastructure of the trilobite material described here is extremely difficult, because in addition to great structural complexity we also have to consider the effects of replacement and diagenesis. We tentatively suggest that in *Ellipsocephalus* the laminae are composed of horizontal sheets of rods with further sheets of material arcing at low angles across the inter-laminae and connecting adjacent laminae. The rods probably represent the original inorganic material of the cuticle, and possibly also reflect the original organic template.

Significance of a finely laminated outer cuticular layer

Many extant arthropods from all the major groups (crustaceans, insects, chelicerates) have an outer cuticular layer with fine lamina units – invariably much finer than those in central regions of their cuticles. This outer layer is very likely to have been formed pre-ecdysially, i.e. under the old cuticle prior to moulting, whereas central and inner regions of the cuticle are usually formed after ecdysis. Possibly slower pre-ecdysial formation in some ways results in the formation of narrow lamina units, but perhaps a functional explanation is more likely. A region of narrow lamina units on the outside of a cuticle will have considerable crack-stopping ability. This holds good with lamination interpreted either according to the Bouligand–Neville model or the Dennell–Mutvei–Dalingwater explanation (for further discussion see Dalingwater 1985, p. 360).

Cavities and canals

The cavities in the outer layer appear circular or egg-shaped in many perpendicular sections, but a few are pear-shaped with the narrower end pointing upwards. Only in sections close to their mid-line do pear-shaped structures reveal their true shape; glancing slices will appear round or oblong. We therefore suggest that the most complex aspect seen reflects the true shape – resembling that of an upwardly pointing pear. The 3 μm canals which characterize the principal layer connect the cavities to the inner surface of the cuticle and therefore originally to the epidermis. On the other hand, the cavities do not quite extend to the surface of the cuticle, nor do they appear to be connected to the surface. However, they extend so close to the surface, that in hand specimens illuminated from above they can be seen through the thin (less than 10 μm) overlying layer of cuticle. Furthermore, slight abrasion will easily remove this overlying layer and expose the tops of cavities.

These cavities and canals are similar in position and dimensions to the Osmólska cavities described and discussed in great detail by Stormer (1980). Størmer considered that this type of cavity occurred below the prismatic layer, but Wilmot (1990*b*) has clearly shown that they usually occur within the prismatic layer. Størmer (1980) suggested a chemosensory function for the Osmólska cavities, whereas Wilmot (1990*b*) preferred to interpret the cavities and canals as some type of modified pore canal. However, the most closely analogous structures to the cavities and canals that we have encountered in an extensive search through the literature are the gland ducts of the millipede *Glomeris convexa* which have dilated tips within a finely-laminated outer region of cuticle (Richards 1951, p. 55, fig. 32C). Gland ducts may be concerned with the secretion and maintenance of the epicuticle. The dilated tips of the gland ducts in *Glomeris* are shown to connect to the surface of the cuticle by minute canals. As mentioned above, we have not detected such openings in *Ellipsocephalus*, but connections to the surface by minute canals would show up only very rarely in sectional slices.

The canals in the endocuticle of *Flexicalymene* which Mutvei (1981, p. 230, fig. 5) termed pore canals have a diameter of about 0·3 μm, similar to that of the pore canals in Recent arthropod cuticles, and do not connect to cavities. They do, however, show a feature of similarity with the canals in *Ellipsocephalus*: disc-like lateral extensions which Mutvei called horizontal lamellae or laminae. They almost certainly reflect ultrastructural elements of the principal layer, but whether they represent the laminae themselves or structures within lamina units is uncertain.

Mutvei (1981, p. 229, fig. 4) described wider ducts, 3–7 μm in diameter, in *Flexicalymene* cuticle. There may also be two types of canal in *Ellipsocephalus* cuticle: the great majority are the 3 μm diameter canals which connect to cavities, but slightly wider canals which do not connect to cavities (e.g. to the right in Pl. 3, fig. 6) may account for the irregularities in the spacing of punctations as seen in surface views of hand specimens and the presence of light circular areas on worn surfaces of hand specimens.

Absence from the outer layer of any structures that can definitely be regarded as pore canals is puzzling. In an outer (and presumably pre-ecdysially formed) layer of cuticle a supply-line for minerals and for other materials required for mineralization would be needed after ecdysis. In Recent decapod crustacean cuticles pore canals almost certainly carry out this function (Roer and Dillaman 1984). However, pore canals are essentially organic structures, so they may not necessarily be preserved as *canals*. Elliptical openings are present on the undersurface of the outer layer (Pl. 2, fig. 4) reminiscent of pore canal pathways: thus pore canals may indeed originally have passed upwards through the *Ellipsocephalus* cuticle outer layer.

Significance of other primary microstructures

Polygonal structures observed at a sub-surface level in the outer laminated layer (Pl. 3, fig. 1) may be equivalent to the interprismatic septa of calcified cuticles of Recent decapod crustaceans. The walls of the septa in these Recent cuticles represent cell margins transformed into cuticular material and show concentrations of cation-binding glycoproteins and maximum carbonic anhydrase activity (Giraud-Guille 1984*b*). Thus the walls represent sites of calcification initiation. It is important to note that they do not extend to the surface of the cuticle and are therefore distinct from polygonal surface ornament whose shapes and sizes are not necessarily related to epidermal cell shapes. Giraud-Guille (1984*b*) has clearly shown that interprismatic septa coincide precisely with underlying epidermal cells.

The thin coating skin (Pl. 1, fig. 1) on the undersurface of the outer layer may represent a deposit of relict organic material from the dissolution of the principal layer. Relict organic material has been identified in other trilobite cuticles by Dalingwater (1973) and Teigler and Towe (1975).

The roughly star-shaped arrays also on the undersurface of the outer layer (Pl. 3, fig. 2) may be the remains of fibrous structures binding together this and the underlying principal layer. Dennell

(1973) identified horizontal arrays of fibres in decapod crustacean cuticles which he suggested might bind together adjacent lamina units.

Secondary microstructures

The 1–2 μm horizontal tubules on the undersurface of the outer layer (Pl. 3, fig. 3) are interpreted as secondary structures because they are irregular in appearance and inconsistent with other cuticular structures in their arrangement. They are remarkably similar in dimensions and appearance to borings described by Runnegar (1985) from shells of the gastropod *Yuwenia bentleyi* from the Lower Cambrian Pavara Limestone of South Australia. Runnegar concluded that these borings were made by cyanobacteria rather than by fungi. Although the nodal structures in the tubules in *Ellipsocephalus* could be interpreted as fungal reproductive bodies, in other aspects the resemblance to the borings described by Runnegar is so close that it seems reasonable to consider the tubules in *Ellipsocephalus* also as infilled borings of cyanobacteria.

Composition of the cuticle in Ellipsocephalus

Although the outer layer is now almost certainly composed of calcium phosphate in the form of apatite and the principal layer (except for the 3 μm canals) of calcium carbonate in the form of calcite, it is uncertain if this reflects the original composition. Teigler and Towe (1975) did, however, demonstrate a high concentration of phosphorus in an outer layer of a Recent crab cuticle. One suggestion that we can make at this stage is that the outer layer may originally have had a different composition from the principal layer, since detailed microstructures are preserved in the former but not in the latter except as discs around perpendicular canals. Alternatively, the outer layer could have had a different structure from the principal layer which was more predisposed to replacement; preferential replacement could have resulted in better preservation of microstructural detail.

We intend to make further studies of the composition of the cuticle employing a range of techniques including cathodoluminescence.

Concluding remarks

Ultrastructural details described here from *Ellipsocephalus* cuticle are the finest so far from any trilobite cuticle and it is ironic that they are possibly also the oldest such details described from any arthropod cuticle. But, before any firm conclusions can be drawn about the general structure of trilobite cuticle, more work is needed on a range of cuticles using careful preparation techniques and taking advantage of the increased resolution of the current generation of SEMs. Parallel studies of Recent crustacean cuticles are also needed to elucidate the precise positional relationships of organic template and inorganic impregnating minerals. There are signs that arthropod cuticle workers are at last breaking out of the straightjacket imposed by the Bouligand–Neville model of cuticular architecture (Neville 1975). Compère and Goffinet (1987*a*, *b*), for example, have described new and exciting structural details, from decapod crustacean cuticles, which do not fit the model. We need to know about and to be able to explain the reasons for differences between the cuticles of different species and of higher taxa, as well as attempting to identify features of similarity.

The significance of the work described and discussed here is not only in the discovery of such exceptionally fine details in a trilobite cuticle, but also in heralding a new phase of fossil arthropod cuticle research made possible by new techniques and new instruments.

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CONTRASTING FEEDING STRATEGIES IN BIVALVES FROM THE SILURIAN OF GOTLAND

by LOUIS LILJEDAHL

ABSTRACT. Two examples of contrasting feeding strategies in bivalves from the Silurian of Gotland are presented. The first shows a deposit-feeding community of protobranchs in which non-siphonate species greatly dominate siphonate ones. This is probably the result of extensive bioturbation by the non-siphonate species causing agitation of the fine-grained sediment and consequent disturbance of the feeding of siphonate species. Tiering of this community is also suggested, based on observations on abundant, silicified material. The second example depicts shallow subtidal life associations of *Ilionia prisca* in preferred orientation. This species shows special characteristics typical of extant deeply burrowing suspension-feeders of the superfamily Lucinacea. It is suggested that *Ilionia prisca* had a unique feeding strategy of anterior inhalation through a mucus tube, and also that it oriented itself obliquely to the direction of wave action, both for optimal intake of suspended food particles and for the avoidance of inhaling its own waste products. Possibly *Ilionia prisca* also lived in symbiosis with sulphur-oxidizing bacteria. The beds discussed are intercalated with shales and it is assumed that the whole bivalve population was instantaneously killed off when smothered by mud.

BIVALVES are perhaps the most thoroughly investigated of all marine invertebrates and many studies have been devoted to the feeding habits of this group. Throughout their evolutionary history, bivalves have occupied a large spectrum of aquatic habitats and are thus well suited for palaeoecological reconstructions.

The feeding habits and trophic relations of benthic invertebrates have been classified by various workers in different ways (e.g. Stanley 1968; Walker and Bambach 1971). Most bivalves are generally considered to be suspension feeders or deposit feeders or carnivores. The classification of organisms as true suspension feeders or true deposit feeders, however, is made difficult by the presence of 'opportunistic feeders', i.e. those capable of using more than one feeding method (Cadée 1984).

Deposit feeders ingest organic matter trapped in the substrate in which they live and therefore must actively move about in search of food. Their gills are simply built and mainly used for respiration, while the collection of food particles is provided by palp proboscides. Siphons, when present, are used for respiration (Cox 1969).

The protobranchs discussed in this paper include one opportunistic deposit feeder, the solemyoid *Janeia silurica* (believed to have been symbiotic with chemoautotrophic bacteria: see Liljedahl 1984*a*, 1984*b*, 1984*c*).

In suspension feeders, the gills are more complex than those of the deposit feeders and are mainly used for food collection. Suspension feeders normally remain fixed in one position and passively feed on particles which come to them through the water. When present, siphons are, in contrast with the deposit feeders, used for feeding. Also within the suspension feeders 'opportunistic' feeders are present. The Silurian *Ilionia prisca* is assumed to have lived in symbiosis with chemoautrophic bacteria and is thus considered an 'opportunistic' filter feeder (Liljedahl in prep.).

Bivalves play an important role in the tiering relationships (relative vertical (ecological) positions of organisms within a community) in many Recent biotas, where different trophic categories or feeding groups may be recognized (Ausich and Bottjer 1984).

The chemical stratification and related environmental changes within a sediment may be

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considerable. Accordingly, the ecological relationships of organisms downwards from the surface can be more extreme below the sediment/water interface than above it.

The first example considered in the present paper, is represented by deposit feeders. In this, community tiering may be established (for detailed analysis see Liljedahl 1985). Indirect competitive interactions may also have been present here: the feeding habits of one trophic group (the non-siphonate deposit feeders) is suggested to have made the substrate unsuitable for representatives of another trophic group, the siphonate deposit feeders (see Rhoads and Young 1970; Levinton and Bambach 1975).

As filterers, suspension feeders are sensitive to sudden environmental changes (in contrast to deposit feeders). Above the sediment/water interface, ecological stratification may also occur, depending on different susceptibility to fouling among the suspension feeders.

The second example is provided by the deeply buried 'opportunistic' suspension feeder *Ilionia prisca* (Hisinger). It inhabited a substrate of low species diversity in a shallow subtidal environment of low oxygen and high sulphur content, unsuitable for most other bivalves. It is suggested that *Ilionia prisca* oriented itself with its anterior-posterior axis obliquely to wave movement, i.e. with its anterior inhalant mucus tube against the flow of suspended food particles. By analogy with its living relatives (Reid and Brand 1986) it is also assumed that *Ilionia prisca* housed chemoautotrophic bacteria in the gills, the bacteria being important nutritional providers for the bivalve (Liljedahl in prep.).

INTERACTIONS BETWEEN THE DEPOSIT-FEEDING BIVALVES OF MÖLLBOS

The material from Möllbos 1 consists of 2743 silicified valves, of which 684 are articulated. Only one specimen (*Nuculodonta gotlandica*) has been observed in life-position (Text-fig. 1G). They were all isolated by acid etching and the preferred life-positions of each of the Möllbos species are thus mainly based on morphological and statistical grounds by analogy with modern counterparts.

One of the advantages of the acid etching method is that the whole preserved shelly fauna is recovered, i.e. all sizes are represented (Liljedahl 1984*a*). Above all it is possible to obtain enough material for fairly reliable statistical processing (Liljedahl 1985).

The bivalves form an important constituent of the Möllbos fauna. Although it is a typical soft-bottom community, this fauna contains a conspicuous amount of sessile benthos such as stromatoporoids, tabulate corals, rugose corals, crinoids, etc. probably due to close vicinity to a reef. It abounds in infaunal burrowers, e.g. protobranch bivalves, gastropods, and annelid worms (Liljedahl 1983).

The Wenlockian Halla Beds at Möllbos consists of a compact, strongly argillaceous calcilutite which is fairly hard due to silicification (Liljedahl 1983, p. 8). The high percentage of deposit feeding

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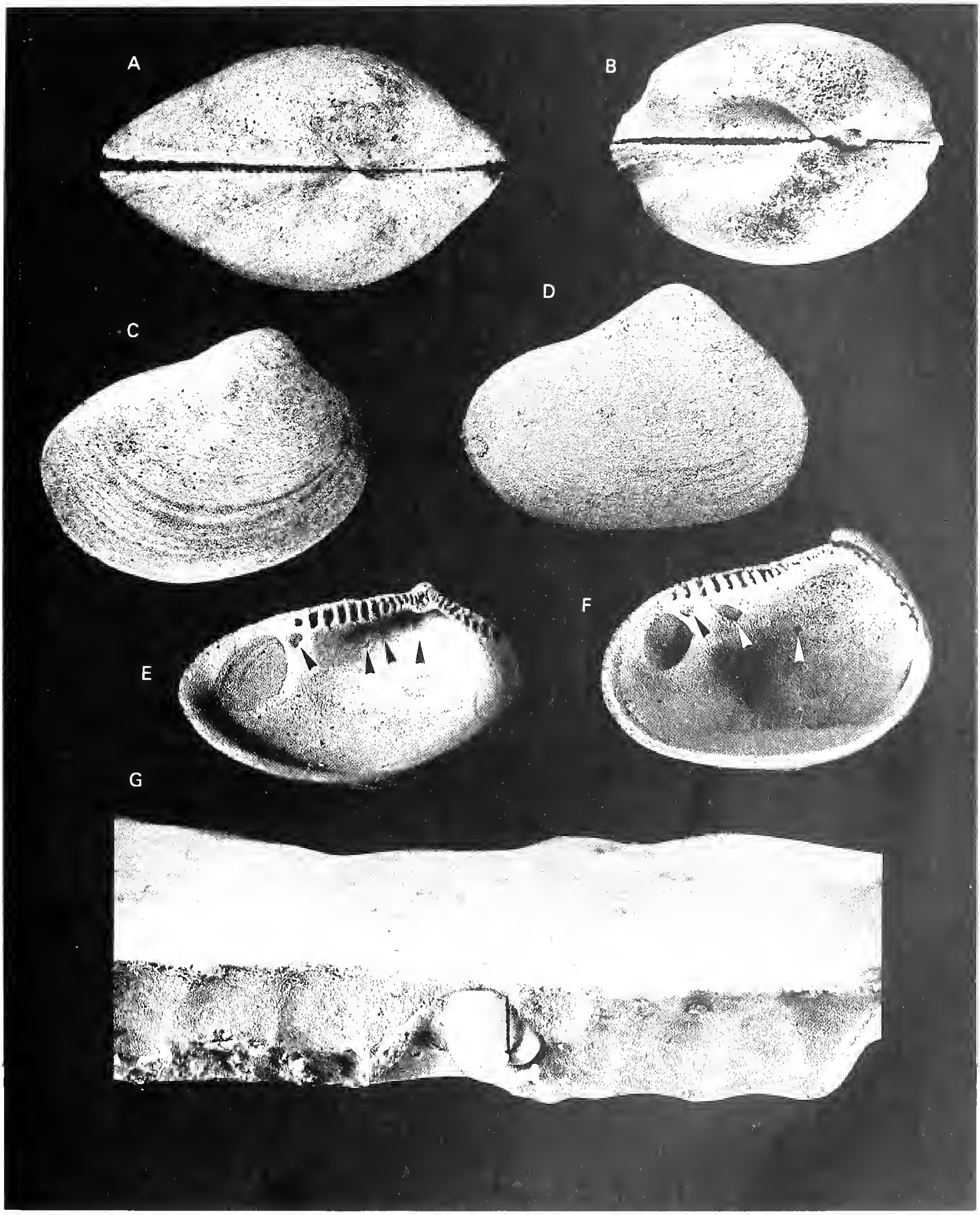
TEXT-FIG. 1. A, *Nuculoidea lens*. External dorsal view of articulated specimen, anterior to the left, SGU TYPES 894, 895, sample G77-28LJ, × 4·3. B, *Nuculodonta gotlandica*. External dorsal view of articulated specimen, anterior to the left, SGU TYPES 1202, 1203, sample G79-82LJ, × 3·9. C, *Nuculoidea lens*. External lateral view of a left valve, SGU TYPE 901, sample G77-28LJ, × 3·9. D, *Nuculodonta gotlandica*. External lateral view of a left valve, SGU TYPE 1036, sample G78-2LL, × 4·4. E, *Nuculoidea lens*. Internal postero-ventral view of holotype (right valve) showing from left to right, anterior adductor muscle scar, anterior pedal protractor muscle scar (first arrow from the left), visceral attachment muscle scar (second arrow), anterior pedal retractor muscle scar (third arrow), and pedal elevator muscle scar (fourth arrow), SGU TYPE 842, sample G77-28LJ, × 3·5. F, *Nuculodonta gotlandica*. Internal posteroventral view of a right valve showing from left to right, anterior adductor muscle scar, anterior pedal protractor muscle scar (first arrow from the left), anterior pedal retractor muscle scar (second arrow), and visceral attachment muscle scar (third arrow), SGU TYPE 1200, sample G79-82LJ, × 4. G, *Nuculodonta gotlandica*. Only specimen of the bivalve fauna of Möllbos 1 found in life-position, just below original sediment surface, LO 6084t, loose boulder, × 1·3. All specimens are silicified and all samples are from Möllbos 1.



TEXT-FIG. 1. For legend see opposite.

animals suggests that this sediment was rich in bacteria, as is often the case in fine grained substrates (Zobell 1938: Newell 1970).

It is concluded that the Möllbos infaunal bivalve fauna is autochthonous and undisturbed except for *post mortem* phenomena, such as disturbances by scavengers and burrowing deposit feeders (Liljedahl 1985; also see Johnson 1960 for criteria for life associations).

The bivalve fauna is numerically dominated by deposit feeding species (90% of the bivalve population: Liljedahl 1985). It comprises four nuculoid species, *Nuculodonta gotlandica* Liljedahl, 1983 (44% of Möllbos bivalves), *Nuculoidea lens* Liljedahl, 1984 (27%), *Palaeostraba baltica* Liljedahl, 1984 (0·7%), *Caesariella lindensis* (Soot-Ryen, 1964) (0·4%), and one solemyoid, *Janeia silurica* Liljedahl, 1984 (18%).

Shell morphology of the different deposit feeding bivalves shows a common theme with minor variations (Liljedahl 1984*a*). The impressions of pedal and other accessory muscles are evident (Text-fig. 1E, F) and the anterior part of the shell is large, indicating a strong and functional burrowing foot (see reconstructions in Text-fig. 3). Also the adductor muscle scars are generally deep, suggesting powerful closing, and thus efficient removal of debris and other indigestible material from the mantle cavity. Much of the space of the mantle cavity was probably occupied by the foot and its muscles, whereas the gills most probably were moderate in size (note the opposite relation in stationary suspension-feeding species).

Shell morphology indicates, in combination with statistical data, a probable life position in the substrate as shown in Text-figure 3. *Nuculodonta gotlandica* has a thick, robust shell, deep adductor muscle scars, prominent pedal muscles scars, and lacks any indication of siphons (Text-fig. 1B, D, F, G). Its shell shape suggests a moderately slow rate of burrowing (Liljedahl 1984*a*, fig. 4). Accordingly, it is proposed that it lived close to the sediment/water interface (Text-fig. 3).

Nuculoidea lens has a somewhat thinner shell, deep adductor muscle scars, clear pedal muscle scars and no indication of siphons (Text-fig. 1A, C, E). The shell shape suggests a moderately slow rate of burrowing (Liljedahl 1984*a*, fig. 4). Most probably it lived somewhat deeper in the substrate than *Nuculodonta gotlandica* (Text-fig. 3; conclusion partly based on articulated valves relative to disarticulated valves; see next section).

Janeia silurica has a thin, elongate and compressed shell and deep adductor muscle scars (Text-fig. 2E–G), all features typical of a rapidly burrowing bivalve (see Liljedahl 1984*a*, fig. 4, 1984*b*). Although fragmented (due to its thin shell), a considerable number of specimens are articulated (31%). Furthermore, the configuration of the muscular impressions suggests that it may have lived symbiotically with chemo-autotrophic bacteria at a sulphide-rich level of the bottom (see Cavanaugh *et al.* 1981) where it did not have to compete for food with other species (Liljedahl 1984*b*). Thus, it seems that of all bivalves of this community *Janeia silurica* inhabited the deepest level (Text-fig. 3).

All three species have an anteriorly expanded shell and a well developed system of pedal muscle scars, just as in extant forms capable of active burrowing.

Palaeostraba baltica has a thin shell with a shape suggesting rapid burrowing (Text-fig. 2B, D; Liljedahl 1984*a*, fig. 4). It also has a posterior sulcus indicating the presence of siphons. Both characters suggest that it lived at a position somewhat below the sediment surface (Text-fig. 3).

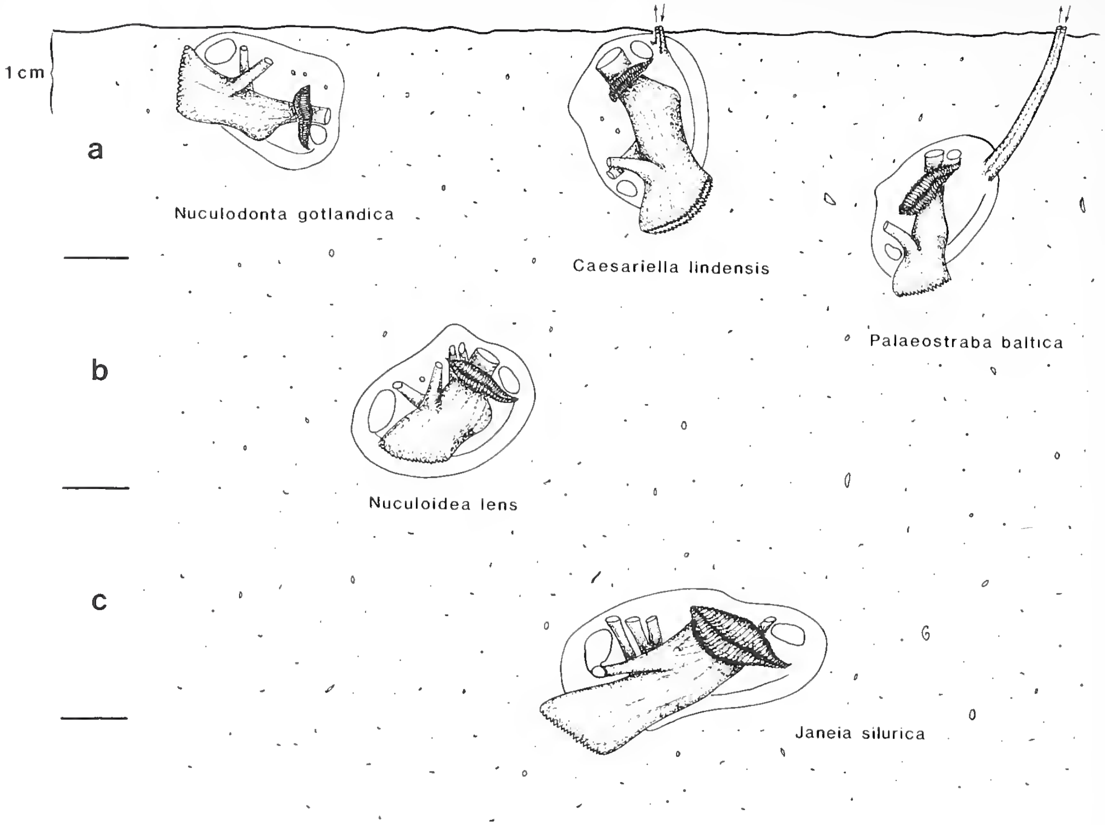
Caesariella lindensis has a thin shell and a shallow pallial sinus containing siphonal retraction muscle scars, which indicates the presence of siphons. Its shell form suggests slow burrowing (Text-fig. 2A, C: Liljedahl 1984*a*, fig. 4) and its life position is thought to have been just below the sediment surface (Text-fig. 3).

The two last mentioned species have conspicuous, but not especially deep, scars of pedal muscles suggesting fairly good burrowing ability.

TEXT-FIG. 2. A, *Caesariella lindensis*. External lateral view of right valve specimen of holotype, SGU TYPE 3606, sample G79-78LJ, × 3·4. B, *Palaeostraba baltica*. External lateral view of holotype (left valve), note posterior sulcus (at arrows), SGU TYPE 3498, sample G78-2LL, × 4·3. C, *Caesariella lindensis*. Internal lateral view of left valve specimen of holotype, SGU TYPE 3607, sample G79-78LJ, × 3·4. D, *Palaeostraba baltica*. Internal lateral view of holotype, × 4. E–G, *Janeia silurica*; E, external dorsal view of articulated specimen, anterior to the right, SGU TYPES 3426, 3427, sample G77-29LJ, × 1·8; F, external lateral view of articulated specimen, anterior to the right, same specimen as E, × 1·7; G, internal lateral view of right valve specimen of holotype, SGU TYPE 3608, sample G79-79LJ, × 2·4. All specimens are silicified and all samples are from Möllbos 1.

TIERING OF THE MÖLLBOS BIVALVE COMMUNITY

Nuculodonta gotlandica makes up 50·0% of the counted 2743 protobranch valves (protobranch shell debris estimated as double that amount), *Nuculoidea lens* 28·7 %, *Janeia silurica* 19·9 %, *Palaeostraba baltica* 0·9 %, and *Caesariella lindensis* 0·4 %.



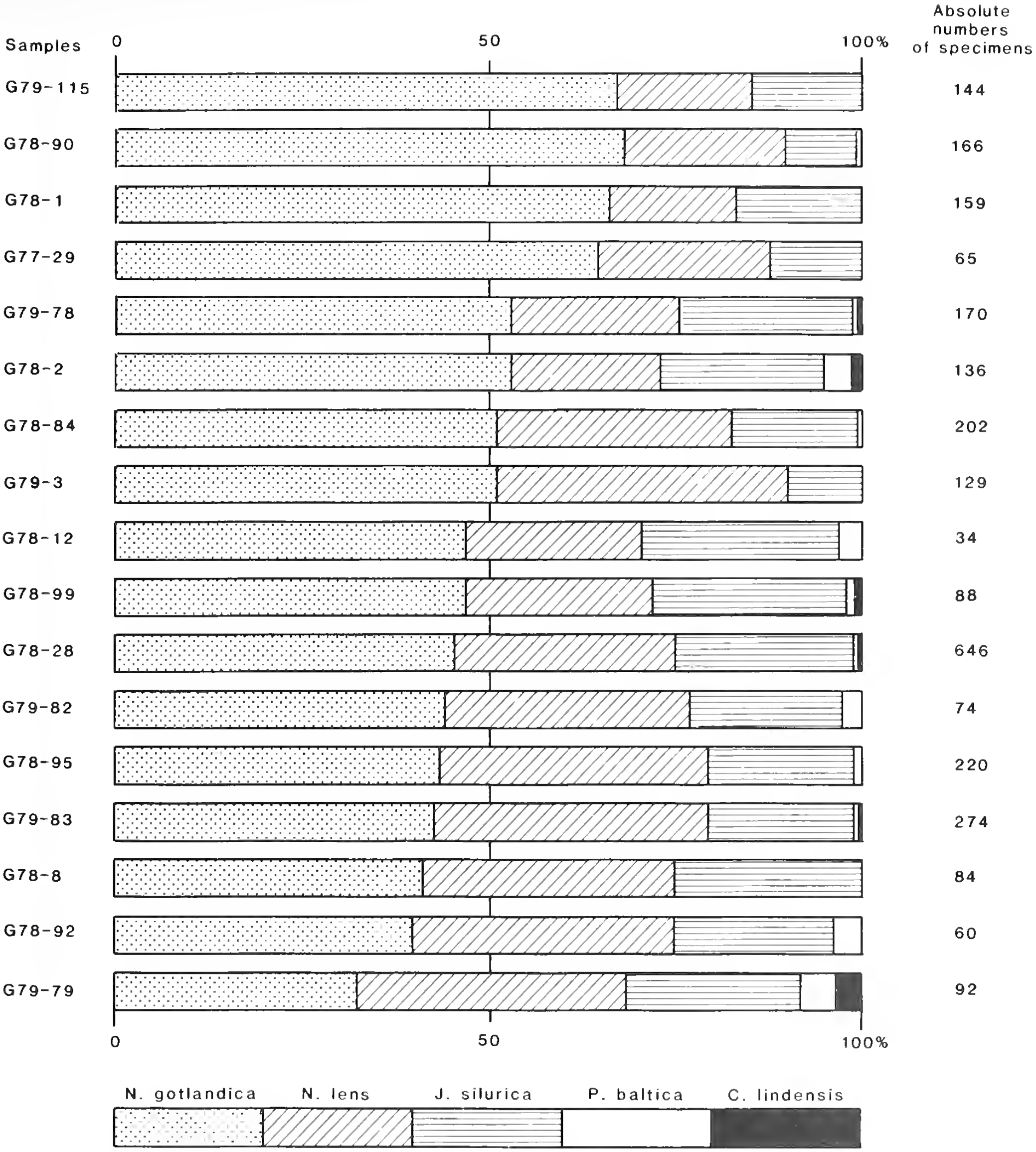
TEXT-FIG. 3. Suggested life-position and reconstructions of the foot and gills of the protobranchs of Möllbos. Arrows indicate in- and exhalant currents, respectively. a, b, and c represent different tiers. Maximum depth approx. 7 cm. Sizes relative to each other.

Seventeen samples were taken from seventeen beds in three vertical sections about ten metres apart. Due to faulting, however, these can not be correlated (Liljedahl 1984*a*, p. 82). The species ranking is shown in Text-figure 4.

Nuculodonta gotlandica is ranked first in sixteen samples and second in one. *Nuculoidea lens* is ranked first in one sample, second in twelve, and third in four. *Janeia silurica* is ranked second in five samples and third in twelve. *Palaeostraba baltica* is ranked fourth in eleven samples and fifth in one. *Caesariella lindensis* is ranked fourth in three samples and fifth in three.

The rates of occurrence of the three most abundant species suggest co-existence at different tiers. Seven samples contain *N. lens* and *J. silurica* in fairly equal numbers and in all the remaining samples but one (G79–3), the difference in occurrence is about 14%. This strengthens the assumption that the various species co-existed but at different tiers with *J. silurica* being the deepest, in a similar manner to the *Nucula proxima* – *Solemya velum* relationship. In the latter *Nucula proxima* is attracted to the burrow openings of *Solemya velum*, representing a positive association (Levinton 1977, p. 208, fig. 13).

N. lens and *J. silurica* also show a significantly higher rate of articulated valves (33·8% and 31·0%, respectively) than *N. gotlandica* (17·9%), indicating a deeper life-position of the two first mentioned. The higher rate of articulated valves of *N. lens*, suggested to have lived at a shallower depth than *J. silurica* and accordingly exposed to more bioturbation, may be explained by its taxodont dentition resisting shearing stresses better than the edentulous hinge of *J. silurica*.



TEXT-FIG. 4. Percentage frequencies of the protobranchs of Möllbos.

The siphonates *Palaeostraba baltica* and *C. lindensis* are greatly outnumbered and together make at most 7·6% of the deposit feeders of this bivalve community. *P. baltica* occurs in twelve samples while *C. lindensis* appears in six. In six of the eight samples in which *N. gotlandica* dominates over *N. lens* and *J. silurica* taken together, *P. baltica* and *C. lindensis* are absent. On the other hand, in eight of the nine samples where *N. lens* and *J. silurica* together dominate *N. gotlandica*, either *P. baltica* or *C. lindensis* or both are present. Thus, *P. baltica* and *C. lindensis* appear to have co-existed with *N. lens* and *J. silurica* and probably inhabited feeding levels different from them, i.e. they occupied the shallowest level, in which *C. lindensis* lived just beneath the sediment/water interface.

Thus when *N. gotlandica* was abundant, the two siphonate deposit feeders were totally crowded out, or almost so. Their feeding activity was probably disturbed by the intense bioturbation of *N. gotlandica* near the sediment surface.

MODE OF LIFE OF *ILIONIA PRISCA* FROM GROGARNSHUVUD

The material from Grogarnshuvud 1, which constitutes the second example, consists of field observations of 151 *in situ* specimens from three separate beds and additional specimens from other beds. All specimens are preserved in calcium carbonate.

Evolutionary aspects

The Lucinacea, constituting an ecologic group of infaunal mucus feeders, hold a unique position in bivalve evolution in being the first known suspension feeders to inhabit a deep life position. They seem to be unrelated to 'normal' siphonate suspension feeders from which they differ through their unusual posterior siphon, their unique anterior inhalant mucus tube, and their anterior-to-posterior flow of water through the mantle cavity (Allen 1958), and in living in symbiosis with bacteria (Dando *et al.* 1986; Reid and Brand 1986).

The earliest representatives of Lucinacea appeared in the Silurian, much earlier than the first appearance of more typical siphonate infaunal bivalves of the Carboniferous. True siphonate suspension feeders, virtually absent in the Palaeozoic, underwent their extensive radiation first in the Mesozoic era (McAlester 1966; Stanley 1968).

Functional morphology

A number of characters of extant Lucinacea are unique among bivalves and some of them may be recognized in *Ilionia prisca* [Hisinger, 1837; original combination *Tellina* (*Lucina*?) *prisca*] as well (Text-figs 5 and 6).

One of the most striking external features is the posterior sulcus (Text-fig. 5C) which in Recent species normally indicates the presence of siphons and also follows the line of attachment of the gills (Allen 1958, p. 427; cf. muscle scars in corresponding position of *Ilionia prisca* in Text-fig. 5B).

Another characteristic is the hypertrophied, linguiform anterior adductor muscle (often conspicuously contrasting in specimens of *Ilionia prisca*, see Text-fig. 5A, B), the surface epithelium of which is ciliated and which sorts the food particles entering by the anterior inhalant tube.

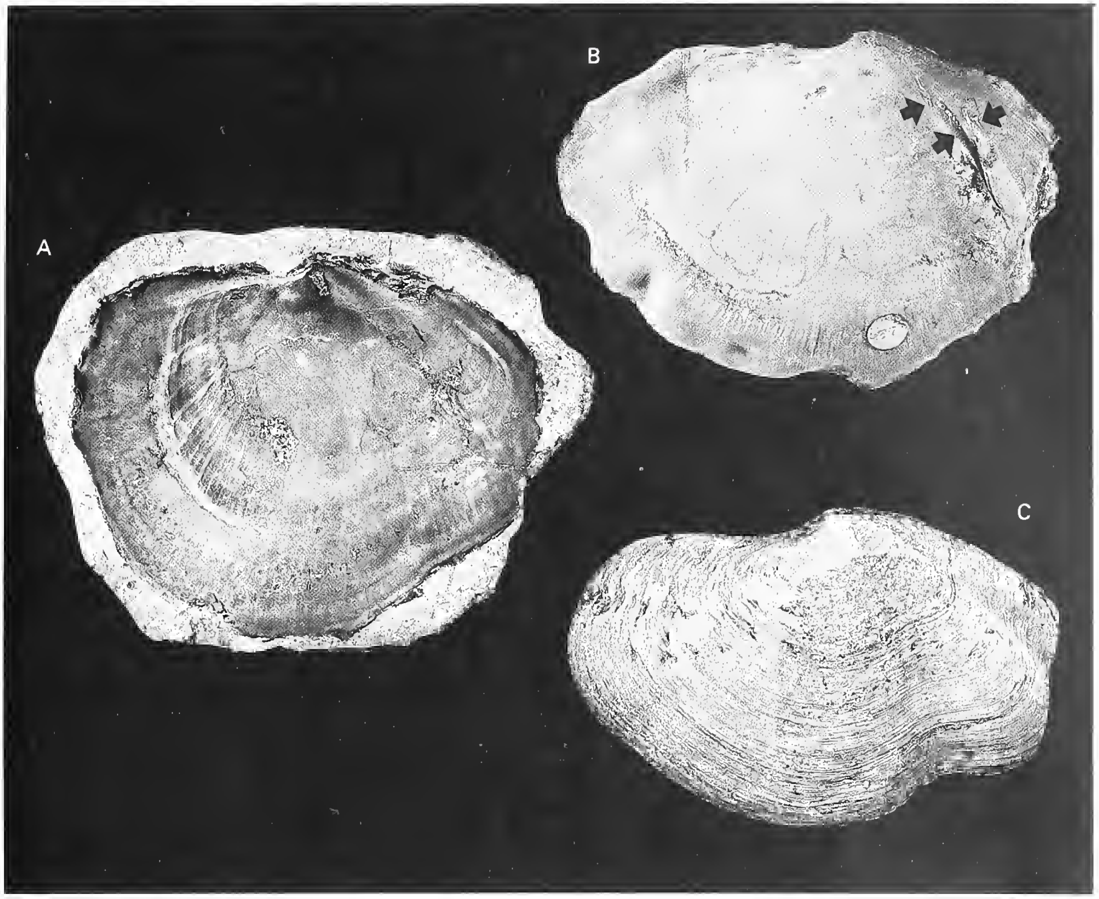
A third characteristic of the Lucinacea is the channel (passage area in *Ilionia prisca*, Text-figs 5B and 6) between the anterior adductor muscle and the pallial attachment of the mantle (pallial line) in which the vermiform part of the foot can operate (Allen 1958, p. 435).

The foot of Lucinacea is highly specialized and in some species it can extend to more than ten times the length of the shell. The mucus inhalant tube is constructed in the sediment by the anterior, vermiform part of the foot. In some species the posterior part of the foot or heel may be protruded and burrowing performed (Allen 1958, p. 448).

Recent lucinaceans lack a posterior inhalant siphon. Instead they have evolved the ability to form an anterior inhalant mucus tube in the sediment. The posteriorly situated exhalant siphon, if present, is unique since no siphonal retractor muscles of normal type (cf. Stanley 1968), are present and therefore no pallial line is formed in the shell (Allen 1958, p. 430).

In soft part morphology the Lucinacea are characterized by a thickened ctenidium consisting of single demibranchs, gill-mantle fusion, the existence of mantle gills and a type V stomach (Purcheon 1958). Finally, representatives of the two families Lucinidae and Thysiridae live in symbiosis with sulphur-oxidizing bacteria (Reid and Brand 1986).

Compared to extant Lucinacea the shell of *Ilionia prisca* is more elongate in antero-posterior direction, due to its extremely elongate anterior adductor muscle. This could also indicate that *Ilionia prisca* was better suited for rapid burrowing. The impressions of the anterior adductor muscle scar are larger and consequently the contractile power of this muscle is likely to have been considerably greater. The conspicuously expanded anterior adductor muscle scar also must have



TEXT-FIG. 5. *Ilionia prisca*. A, internal view of a single right valve, note conspicuous anterior adductor muscle scar, RMMO 17790, Östergarn, Ludlovian Hemse Beds, × 1·2. B, lateral view of internal mould of articulated specimen, anterior to the left, note gill attachment muscle scars (arrowed) and radial muscle scars of the mantle edge, note also space between the anterior adductor muscle scar and pallial line, RMMO 149879, Östergarn, Ludlovian Hemse Beds, × 1·2. C, external lateral view of a single left valve, RMMO 158171, Histilles, Ludlovian Hemse Beds, × 1.0.

reduced the space available for the gills, which were comparatively smaller than those of its living relatives. This could have resulted in a less efficient sorting ability of the gills as compared to its Recent relatives.

On the other hand, if the greatly extended ventral part of the anterior adductor muscle (the muscle scar being considerably larger than in modern lucinaceans) acted as a sorting area for inhaled particles, this could have compensated for smaller sized gills.

Ilionia prisca is integripalliate, as are Recent lucinaceans, but is believed to have had a posterior exhalant siphon, as indicated by the conspicuous external posterior diagonal sulcus (cf. Allen 1958, p. 449).

In some specimens the ventral margin is undulating. This feature, also present in for example *Grammysia*, in combination with the elongate shell form may have helped in rapid downward burrowing (see Bambach 1971; Marsh 1984).

The Silurian *Ilionia prisca* shows such remarkable conformity with living Lucinacea that it may safely be assumed that *Ilionia prisca* had adopted the unusual lucinacean life habit (see McAlester 1965), a mode of life already initiated in Ordovician times by the genus *Babinka*. In addition to the suspension feeding habit, *Ilionia prisca* possibly also housed sulphur-oxidizing bacteria in its gills, in analogy with its living relatives (cf. Reid and Brand 1986).

Life habit

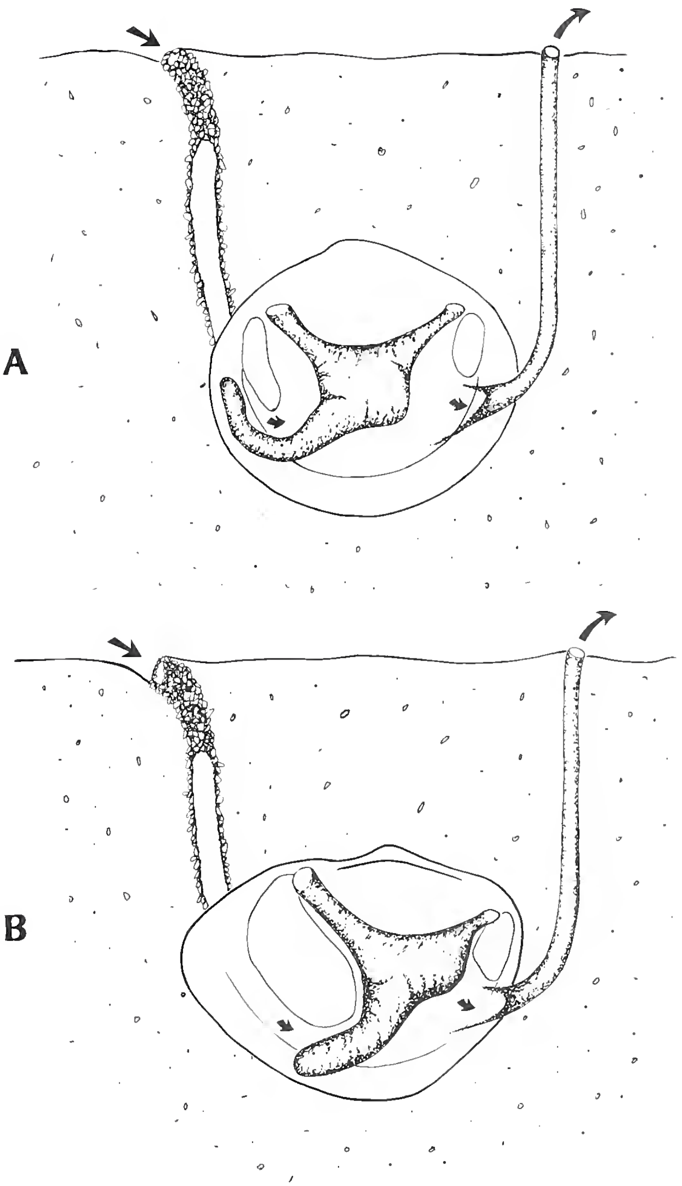
Extant Lucinacea are uniquely adapted for deeply burrowing suspension-feeding in environments with a low oxygen and a high sulphur content (Southward 1986). In their gills they have chemoautotrophic endosymbiotic bacteria (sulphur-oxidizing) which act as important nutritional providers for the bivalve (Berg and Alatolo 1984; Spiro *et al.* 1986). Some authors consider this symbiosis to be the main feeding mode (Reid and Brand 1986).

Besides the bacterial symbiosis the lucinaceans feed in the following way (Text-fig. 6A). In a deeply buried position, nutrient-laden water is drawn into the mantle cavity through an anterior mucus-lined tube in the sediment, made by the vermiform part of the foot. The water passes the ciliated ventral part of the anterior adductor muscle which acts as a sorting area before the water reaches the gills. The exhalant water with indigestible particles is expelled posteriorly by rapid contraction of the adductor muscles, in some species through a posterior siphon to the sediment surface, in others directly into the sediment (Allen 1958).

Based on comparative anatomy with its Recent descendants (Allen 1958), it is concluded that *Ilionia prisca* was a deeply burrowing, shallow subtidal suspension feeder (Text-fig. 6B). *Ilionia prisca* lived in a soft, carbonate mud of low oxygen and high sulphur content, bioturbated to the extent that the original lamination is completely lost (Sundquist 1982, p. 87). In equivalent sediments today the diversity of suspension-feeding bivalves is commonly low (Buchanan 1958; Rhoads 1970; Rhoads and Yonge 1970). Indeed, species diversity is low at Grogarnshuvud 1 (see Sundquist 1982, p. 88), including only three additional bivalve species, an undescribed, epi-byssate suspension feeder, a protobranch nuculoid and the protobranch solemyoid *Janeia silurica*. The suspension feeder (found as disarticulated valves only) was most probably exotic and transported into the present bivalve community together with empty orthocone nautiloid shells during ephemeral events (see Rhythmic trapping, below). Alternatively, if it belonged to the present bivalve community, it may possibly have occupied a high level, epi-byssate position.

The presence of protobranchs indicates a high organic content in the original substrate. Extant Lucinacea generally live in environments where the food supply is so low that all available food particles must be accepted (Allen 1958, p. 480). This is achieved by their specialized sorting mechanism with the help of symbiotic bacteria. The suggestion of similar conditions at this locality at the time of sedimentation seems reasonable. The assumed low oxygen and high sulphur content of the substrate at Grogarnshuvud 1 might explain the low bivalve diversity with only two additional infaunal bivalve species, the deepest one, *Janeia silurica*, also assumed to have had symbiotic sulphur reducing bacteria (by analogy with its living relatives). *Ilionia prisca* most probably had a specially developed sorting mechanism as well as a strong adductor muscle, capable of powerful retraction and closure of the valves for efficiently discharging indigestible particles posteriorly. Its deep life position suggests that it lived in the oxygen-poor, sulphur-rich zone of the sediment, which strengthens the idea of a symbiosis with anaerobic bacteria. Other lucinid-solemyid associations have also been connected with fine-grained and poor-food habitats, e.g. the Cenozoic *Thyasira–Lucinoma–Solemya* association (Hickman, 1984).

Feeding capacity is one of the most important features upon which selection pressure acts in animal species (Stanley 1970, p. 79), and it appears that the unique feeding strategy of *Ilionia prisca* (a deep life position with an inferred anterior inhalant tube and a posterior exhalant system in combination with symbiosis with sulphur-oxidizing bacteria), seems to have been an optimal adaptation to an environment hostile to all other infaunal suspension feeding bivalves.

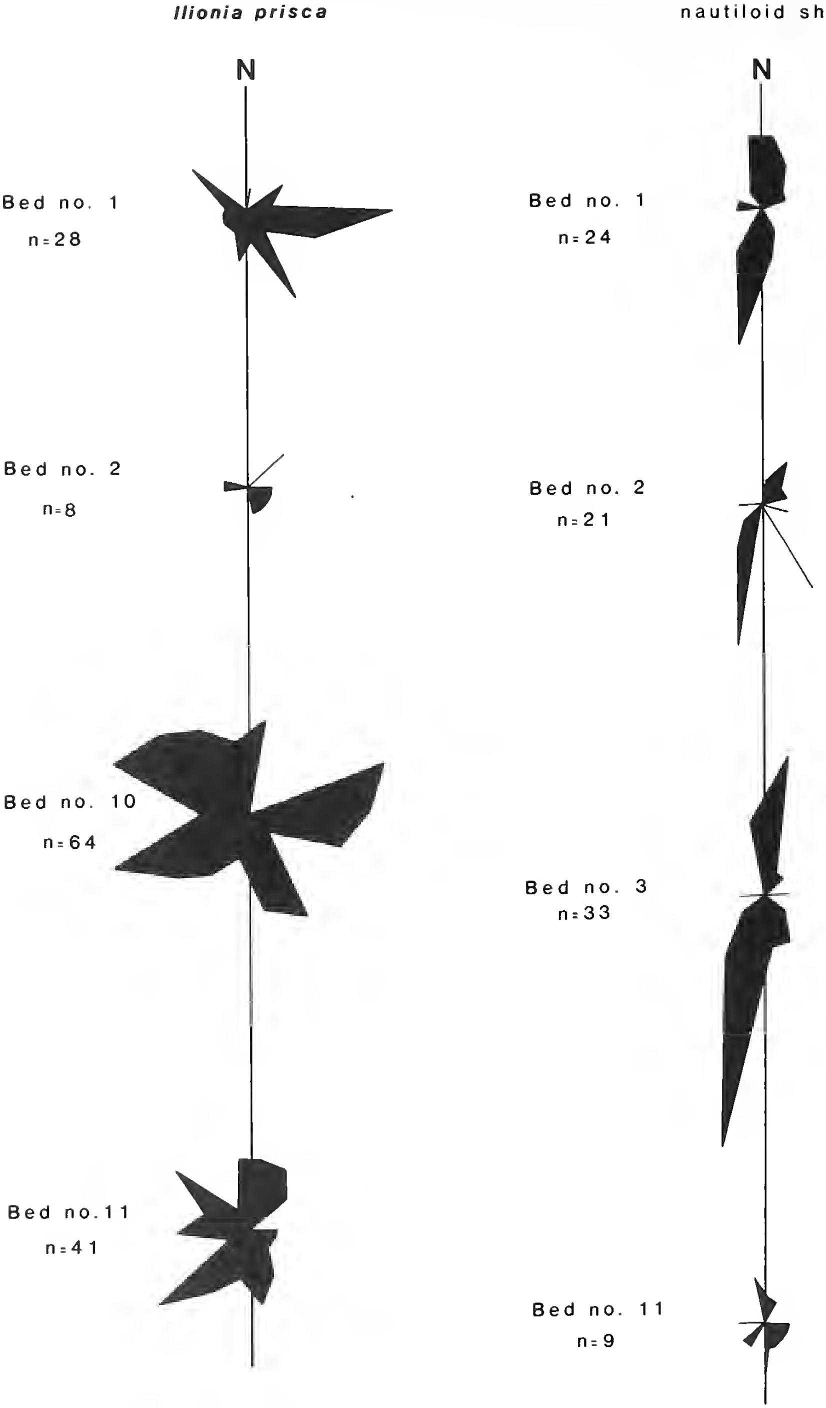


TEXT-FIG. 6. A, life position of Recent lucinacean bivalves (modified after Allen 1958; McAlester 1965); the foot, the sites of the adductor muscles (stippled) and the posterior exhalant siphon are shown. B, suggested life position and reconstruction of the foot and posterior exhalant siphon of *Ilionia prisca* (muscular impressions stippled); water is inhaled through a mucus lined tube; arrows indicate direction of water flow.

Preferred orientation

Grogarnshuvud 1 includes a series of beds of interlayered fine grained limestones and calcareous shales belonging to the Hemse Beds, units *c* and *d* (for detailed descriptions see Sundquist 1982).

At several horizons a large number of *in situ* specimens of *Ilionia prisca* can be observed contrasting conspicuously with the recently eroded bedding planes. In four of the beds abounding in *Ilionia prisca* (Nos 1, 2, 10, 11) the orientation of the bivalves was measured. In three of these



TEXT-FIG. 7. Rose diagram of direction of anterior end showing orientation of anteroposterior axis of *in situ* specimens of *Ilionia prisca* and of orthocone nautiloid shells on bedding planes at Grogarnshuvud 1. n = numbers of specimens.

beds (Nos 1, 2, 11) and an additional bed (No. 3 with less abundant *Ilionia prisca*) the orientation of orthoconic nautiloid shells was recorded. The results are presented in Text-figure 7.

Sundquist (1982, p. 85, fig. 4) made a similar study of nautiloid shell orientation in this locality. Bed No. 1 probably corresponds to Sundquist's No. 4, bed No. 2 to his No. 3, and bed No. 3 to his No. 2. Bed No. 10 lacks nautiloid shells while in bed 11 there are only eight recorded specimens.

In addition to the bivalve specimens *in situ* on the bedding planes a number of *in situ* specimens were found well within the limestone beds.

In principle the bivalves exhibit a quadro-polar, preferred *in situ* orientation with their anterior end pointed in approximately NW, SE, ENE, WSW directions, which seem to be consistent throughout the beds at this locality (Text-fig. 7). In bed No. 1 there is a dominant direction to the E, in bed No. 2 a dominant direction to the SE, whereas bed No. 11 lacks a dominant anterior direction to the SE.

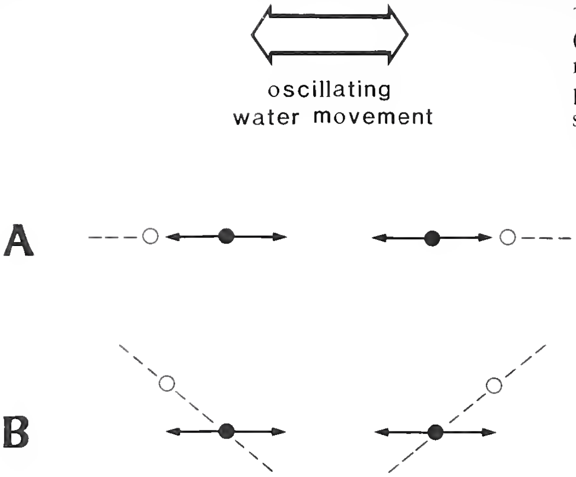
Discussion. Some bivalves have evolved the behaviourial strategy of orienting themselves in a direction favourable for feeding. A few commensal species of Erycinacea, for example, orient themselves with their anterior end (where the inhalant siphon is situated) towards their host, due to chemokinetic response (Morton 1962). Other species of the same family are able to orient themselves with their anterior end to stimuli of light, gravity and lateral contact (Morton 1960). Some burrowing bivalves orient themselves preferentially with their posterior siphon against the prevailing current direction. For example, the alignment of *Anadara trapezia* is correlated with the direction and strength of tidal or wind-driven water currents (O'Gower and Nicol 1971). It is assumed that correct orientation of this bivalve would assist respiration, feeding and sanitation, and would possibly also lessen the chances of accidental dislodgement (O'Gower and Nicol 1971, p. 277). Some fresh-water bivalves also show preferred orientation in relation to water currents (J. Kříž, pers. comm. 1988).

As far as the orientation of *Ilionia prisca* is concerned, it may be related directly to the alignment of the orthocone nautiloid shells on the same bedding planes or to a factor which affected both the bivalves and the empty cephalopod shells. Sundquist (1982) concluded that the bipolar apex orientation of the nautiloid shells indicates a preferred orientation caused by wave action. The orientation pattern does not, however, form two completely opposing maxima, and is interpreted as the result of interacting forces of waves and wave currents. The wave progression is suggested to have been from ESE (Sundquist 1982, p. 85).

The orientation of the nautiloid shells in this paper (Text-fig. 7), agrees with those in Sundquist's study, thus strengthens the assumption of a fairly constant main wave progression from the ESE in this area at the time of sedimentation.

Assuming that the different beds at this locality were deposited under fairly constant conditions (Sundquist 1982, p. 86), the stable uniform orientation of the nautiloid shells may be taken as a criterion of a constant shore line direction, parallel to the anterior-posterior axis of the shells. Although caution should be taken in interpretations of palaeogeography based on locally restricted material, the shore line at this locality, as indicated by the elongated shells of nautiloids and gastropods, at the time of sedimentation seems to have been aligned roughly NNE–SSW. This direction agrees fairly well with earlier reconstructions of shore lines and palaeobathymetry on Gotland (Hadding 1958, Manten 1971, Laufeld 1974, Eriksson and Laufeld 1978, Bergman 1979, Sundquist 1982).

The orientation of the length axis of the bivalves of each individual bed at this locality is fairly constant, which is also the case with the nautiloid shells, indicating a wave progression direction from the ESE. Thus, it seems as though *Ilionia prisca* oriented itself with its anterior-posterior axis oblique to the prevailing wave direction, in which the suspended (food) particles travel. If so, its anterior inhalant mucus tube was facing the net transport of food particles (Text-fig. 8B; cf. similar life position of *Thyasira* and *Lucinoma* with the opening of their anterior mucus tube facing the current at the sediment/water interface, in Hickman 1984, fig. 9). Probably this orientation was more advantageous than if the bivalves were aligned in the same direction as water movement (Text-



TEXT-FIG. 8. Orientation of anteroposterior axis (broken lines) of *Ilionia prisca* in relation to water movement. Anterior inhalant tube (open circle) and posterior exhalant siphon (filled circle), thin arrows showing direction of waste products. A, hypothetical in line-orientation. B, observed oblique orientation.

fig. 8A). In the latter case, with an oscillating wave movement, the chances of inhaling its own waste products are greater than in case of oblique orientation.

Rhythmic trapping

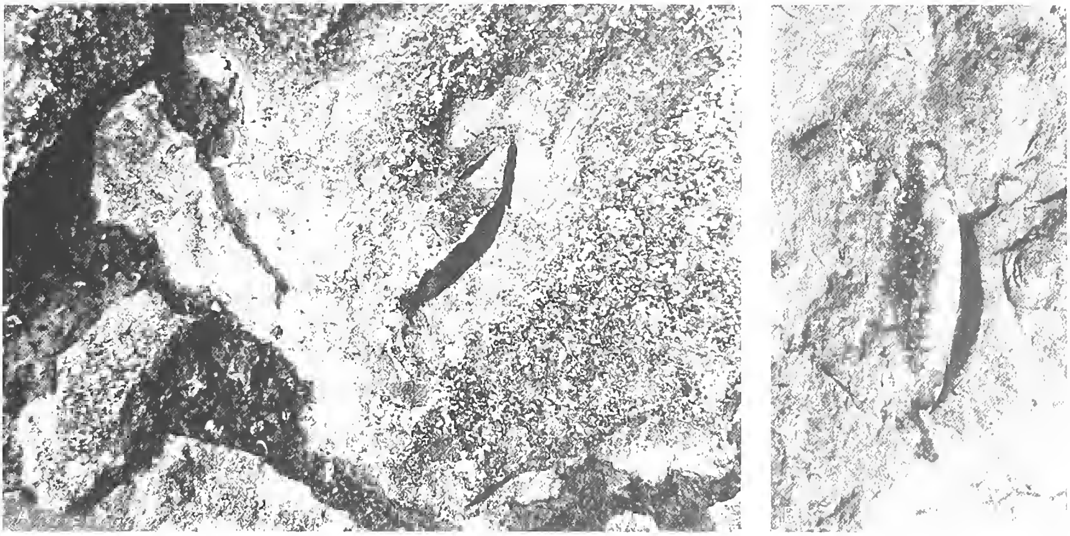
A number of the limestone beds at Grogarnshuvud 1 abound in *Ilionia prisca* while others contain few or no specimens. Each of the beds discussed is intercalated with calcareous shales. The thickness of the limestone beds ranges from 70 to 130 mm. The shales are usually 10 mm thick but can in places reach 60 mm (see also Sundquist 1982).

It is suggested that each limestone bed represents one life association of *Ilionia prisca*, although there is a conspicuous lack of juvenile specimens (Liljedahl, in prep.).

Sundquist (1982, pp. 87–89) assumes that the calcareous shale beds represents the final stage of a previous ephemeral incident, such as a storm, etc. The shales were deposited rhythmically and possibly some of them represent volcanic ash-falls rich in silica, indicated by the presence of silicified fossils. On such occasions a large number of floating nautiloid shells were stranded and oriented parallel to the shore due to storm-wave action. The water was heavily loaded with suspended particles, which eventually came to rest, resulting in a deposit considerably thicker than the present thin shale beds. The fouling of the water and/or sedimentation of the fine grained material most probably was catastrophic for the bivalves and the infaunal species were forced to escape.

However, when overburden stress reaches a critically high value, burrowing infaunal organisms can not escape burial. Experiments on living polychaete/bivalve communities show that this value (40 Kpa) corresponds to a burial depth of *c.* 28 cm (Nicols *et al.* 1978). Specimens of *Ilionia prisca* are found down to a depth of 10 cm or more in the sediment and with an overburden of a thick layer of clay (now considerably compacted). This limit could have been reached in the present community at Grogarnshuvud 1 and the infaunal bivalves fatally trapped. It seems as if no reworkers, including protobranch bivalves, gastropods, annelid worms etc. survived, since *Ilionia prisca* was preserved undisturbed in 'life' position.

As stated, specimens of *Ilionia prisca* have been found at different depths in the beds and even at the sediment surface (all orientation-measured specimens). A number of individuals are inclined, with their antero-posterior axis dipping at an angle of 10–15° to the bedding plane (Text-fig. 9). This suggests that these individuals were killed during the rocking movement of burrowing, perhaps while attempting to escape. According to Stanley (1972) and Nicols *et al.* (1978), in a series of experiments, individual burrowing ability of each bivalve species resulted in differences in escape efficiency. Although no escape structures have been found in the different beds at Grogarnshuvud, the slurry-like nature of the sediment may account for their absence.



TEXT-FIG. 9. *In situ* specimens of *Ilionia prisca* on eroded bedding surfaces, Grogarnshuvud 1, Ludlovian Hemse Beds. A, articulated specimen preserved as internal mould of surrounding sediment, ×0.6. B, articulated specimen preserved as druse filled internal mould, ×0·7.

The specimens found on the bedding planes either: (1) succeeded in escaping burial; their gills were, however, eventually clogged due to the large amount of fine grained suspension in the very turbid water; or (2) they were killed in 'life' position, or rather 'death' position after having burrowed themselves downwards in the sediment and later isolated by erosion caused by the ephemeral violent event. The presence of some specimens, preserved as drusy filled cavities (Text-fig. 9B), supports this latter assumption. They indicate extremely rapid burial and enough compaction forces to prevent the ligament to open the valves after soft part corruption.

The absence of *Ilionia prisca* from some of the beds may result from the sedimentation of the fine grained material not being rapid enough for catastrophic burial. Alternatively the high turbidity event may have been too short for the bivalves to be suffocated. In either case the bivalves might have been able to escape and survive. It is also possible that the bivalves had not yet colonized the area after the previous catastrophic event.

It seems as if only one or a few age classes colonized the area after each previous mud sedimentation event. Presumably either these individuals were killed during the following catastrophic incident before they were able to reproduce, or the environment was simply unfavourable for their young offspring (see Rhoads and Young 1970).

Repository. Specimens with their numbers prefixed RMMO are deposited in the type collection of the Swedish Museum of Natural History, Box 50007, S-104 05 Stockholm, Sweden, those prefixed SGU TYPE are deposited in the type collection of the Geological Survey of Sweden, Box 670, S-751 28 Uppsala, Sweden, and those prefixed LO in the type collection of the Geological Institute, Lund University, Sölvegatan 13, S-223 62 Lund, Sweden.

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LIZARD EGG SHELLS FROM THE LOWER CRETACEOUS OF CUENCA PROVINCE, SPAIN

by ROLF KOHRING

ABSTRACT. The Lower Cretaceous vertebrate-bearing coaly marls and limestones of Uña (Province of Cuenca, Spain) have yielded fragmentary reptilian egg shells. The shell is of gekkonid microstructure type, and thus they can be confidently assigned to the lizards. These fragments represent the oldest known gekko-like egg shells.

FOSSIL egg shells have been reported nearly worldwide, especially from Upper Cretaceous and Tertiary deposits, and they have been assigned, according to their microstructure and biomineralization, to turtles, crocodiles, dinosaurs, and birds (reviewed by Hirsch and Packard 1987). Fossilized egg shells of snakes and lizards, however, are only rarely described, owing to their largely non-mineralized composition; nearly all squamates produce eggs with soft shells consisting of interlacing protein fibrils and some calcareous matter, probably homologous to the membrana testacea of avian eggs (Schleich and Kästle 1988). Only the recent gekkonids (Lacertilia) develop calcified (and thus fossilizable) rigid egg shells, characterized by a continuous layer, composed of tightly abutted jagged columns, and surface nodes. The thickness of both fossil and recent gekkonid egg shells ranges from 35 to 280 μm (Schleich and Kästle 1988).

Fossil gekko-like egg shells are reported from the Lower Miocene of Kenya (Hirsch and Harris 1989), the Oligocene of the Mainz Basin (Schleich and Kästle 1988), the Lower Eocene of Wyoming (Hirsch and Packard 1987), the Cretaceous/Tertiary-boundary of Peru (Hirsch in Mourier *et al.* 1988), the Upper Cretaceous of both Montana (Hirsch and Quinn, in press) and India (Sahni *et al.* 1984), and the Lower Cretaceous of Mongolia (Alifanov 1989). One genus (*Ilerdaesaurus* sp.) of this material is under study by A. Richter (Berlin). According to Hoffstetter (1964) gekkonids are known since the Upper Jurassic. The lizards of Uña are not yet described (Krebs, pers. comm.)

LOCALITY AND STRATIGRAPHY

The coal-bearing marls and limestones of Uña (province of Cuenca, Spain) have yielded tetrapods, especially frogs (Fey 1988), turtles and lizards (Krebs, pers. comm.), crocodiles (Brinkmann 1989), and early mammals (Henkel and Krebs 1969). They have been dated as Upper Barremian on the basis of palynomorphs (Mohr 1989), ostracodes, and charophytes (Schudack 1989). The palaeoenvironment of Uña is postulated to have been lacustrine, with marshy, deltaic deposits (Gierlowski-Kordesch and Janofske 1990). The egg shells described here are well preserved; only their margins are partially pyritized, as is typical also for the gastropods, ostracodes, and charophytes of Uña.

THE MATERIAL

Description

In all, eight tiny, dark brown coloured shell fragments (5 × 10 mm), embedded in the coaly sediment, have been studied in thin sections and by scanning electron microscopy (SEM, Cambridge Stereoscan 360). In thin section, the egg shells display a continuous layer with hardly visible fine, closely spaced growth-stage lines and a light coloured secondary layer in the outer part, which is obviously a diagenetic structure (Hirsch, pers.

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comm.) (Pl. 1, fig. 5). It is never pyritized in any of the specimens. In XPL an extinction pattern with cone-shaped wedges in the upper part of the primary layer and partially in the secondary layer is visible.

In SEM studies, some further morphological features can be observed. The shell consists of a nearly complete homogenous calcitic layer without recognizable shell units (Pl. 1, figs 2 and 6), and therefore is very similar to the recent gekko *Ptyodactylus* (Schleich and Kästle 1988). In its upper part, the 20 μm thick secondary layer with horizontal crystallites is visible (Pl. 1, fig. 4). This characteristic structure has been mentioned also from Upper Cretaceous gekko-like egg shells of Montana (Hirsch and Quinn, in press) and from hadrosaurian egg shells (Hirsch and Packard 1987). The surface is covered with a thin 3 μm mineralized layer, as is typical for nearly all recent gekkos (Schleich & Kästle 1988). However, this layer has never been reported from fossil lizard eggs. The shell thickness, including surface nodes, is 170–180 μm. The diameter of these nodes is about 100 μm (Pl. 1, fig. 1).

Discussion

Other distinctive reptilian egg shell microstructures, such as pores, pore openings, and basal aragonitic mammallae could not be found. Probably the rigid gekkonid egg shell is not homologous to those of other reptiles or birds.

The remarkable structural similarities to modern gekkonid egg shells allow the assignment of the Uña material to the lizards. These late Barremian fragments are the oldest known certain lizard egg shells. Due to the poor knowledge of the problematic diagenetic pattern of egg shells an identification of the very thin outer layer as a mineralized organic cover seems hitherto impossible. The fragmentation of the shells suggests substantial transport. The primary shapes and sizes of the eggs cannot be reconstructed.

A single thin-shelled (about 50 μm) fragment is known from the Upper Jurassic (Kimmeridgian) coaly marls and limestones of Guimarota (Central Portugal), where turtle egg shells have been described (Kohring 1990). It is similar in microstructure to recent gekkonid egg shells, but its real taxonomic position is uncertain (Pl. 1, fig. 8).

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EXPLANATION OF PLATE 1

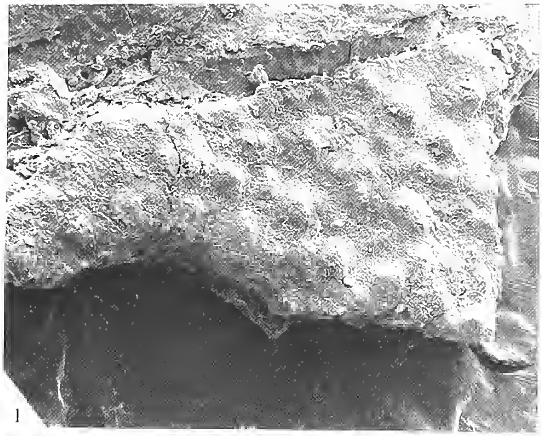
Figs 1–6. Lizard egg shell fragments from the Lower Cretaceous of Uña. 1, outer surface with nodes, × 50. 2, lateral view with homogenous calcitic layer, secondary layer, outside is up, × 100. 3, lateral view, note secondary layer, × 200. 4, Secondary layer, × 400. 5, lateral view in thin section in ordinary light, outside with a secondary layer is up, note pyritized margins, × 50. 6, lateral view, × 80.

Fig. 7. Recent gekko egg shell, *Tarentola* sp., lateral view with nodose outer surface, × 300.

Fig. 8. Uncertain gekko-like egg shell from the Upper Jurassic of Guimarota, lateral view, × 300.

Specimens are housed in the Institut für Paläontologie, Freie Universität Berlin under the registered numbers Un Bar ES 1–8.

PLATE 1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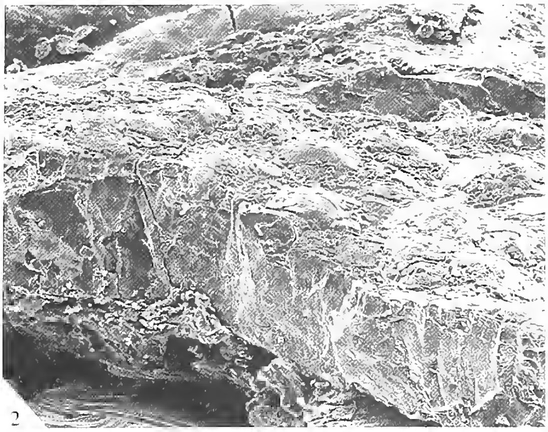
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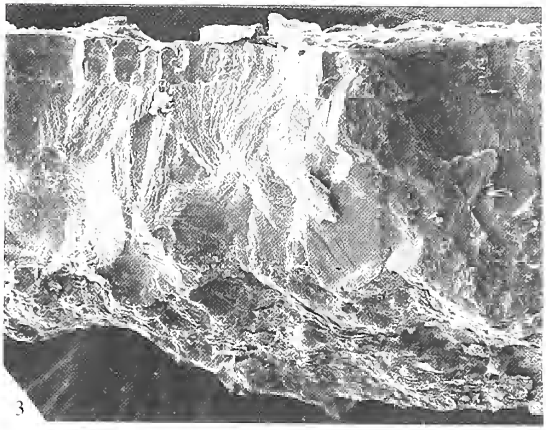
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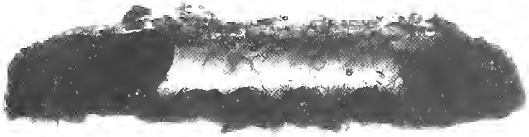
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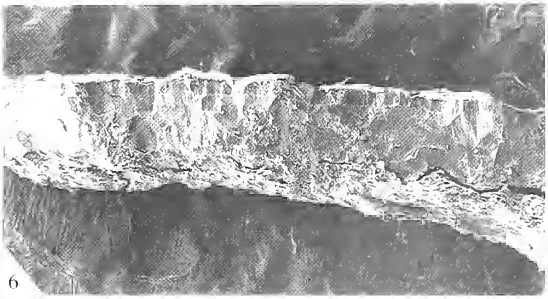
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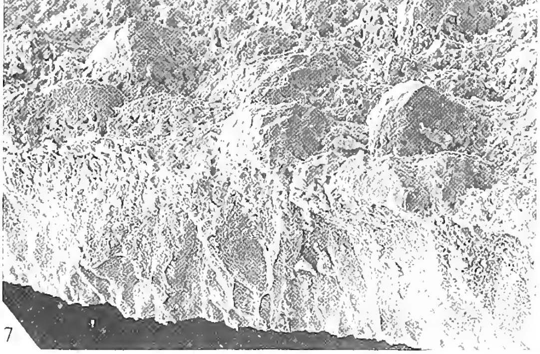
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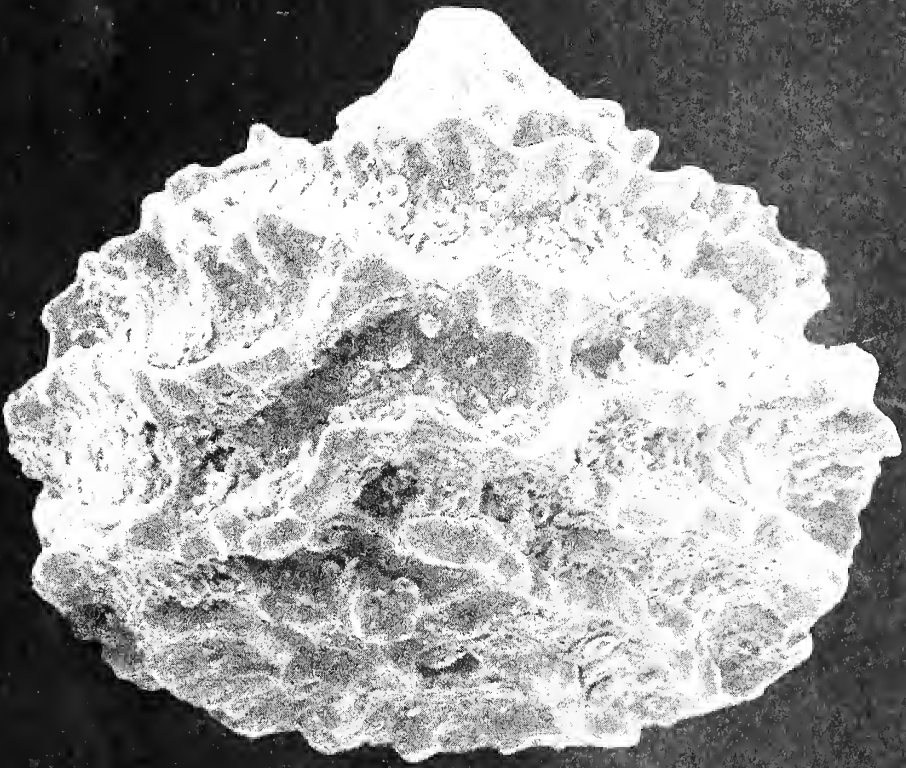

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Cover: *Bolboforma intermedia* Daniels and Spiegler (Incertae Sedis, possibly a calcified algal cyst) from Site 552A, southwest margin of Rockall Plateau, late Miocene NN9–10. × 800. *Bolboforma* was planktonic and cysts are found in epicontinental shelf sea deposits, thus providing a useful biostratigraphic link with oceanic sequences.

A SPIDER AND OTHER ARACHNIDS FROM THE DEVONIAN OF NEW YORK, AND REINTERPRETATIONS OF DEVONIAN ARANEAE

by PAUL A. SELDEN, WILLIAM A. SHEAR *and* PATRICIA M. BONAMO

ABSTRACT. The oldest known spider, from the Devonian (Givetian) of Gilboa, New York, is *Attercopus fimbriunguis* (Shear, Selden and Rolfe), parts of which were originally described as a trigonotarbid, possibly of the genus *Gelasinotarbus*. Previous reports of Devonian spider fossils, from the Lower Emsian of Alken-an-der-Mosel, Germany, and the Pragian of Rhynie, Scotland, are shown to be erroneous identifications. *Attercopus* is placed as sister-taxon to all living spiders, on the basis of characters of the spinneret and the arrangement of the patella–tibia joint of the walking legs. A cladogram of the relationships of all pulmonate arachnids is presented. A pulmonate arachnid from Gilboa, related to Araneae and Amblypygi, is described as *Ecchosis pulchribothrium* Selden and Shear, gen. et sp. nov., and additional arachnid material is described.

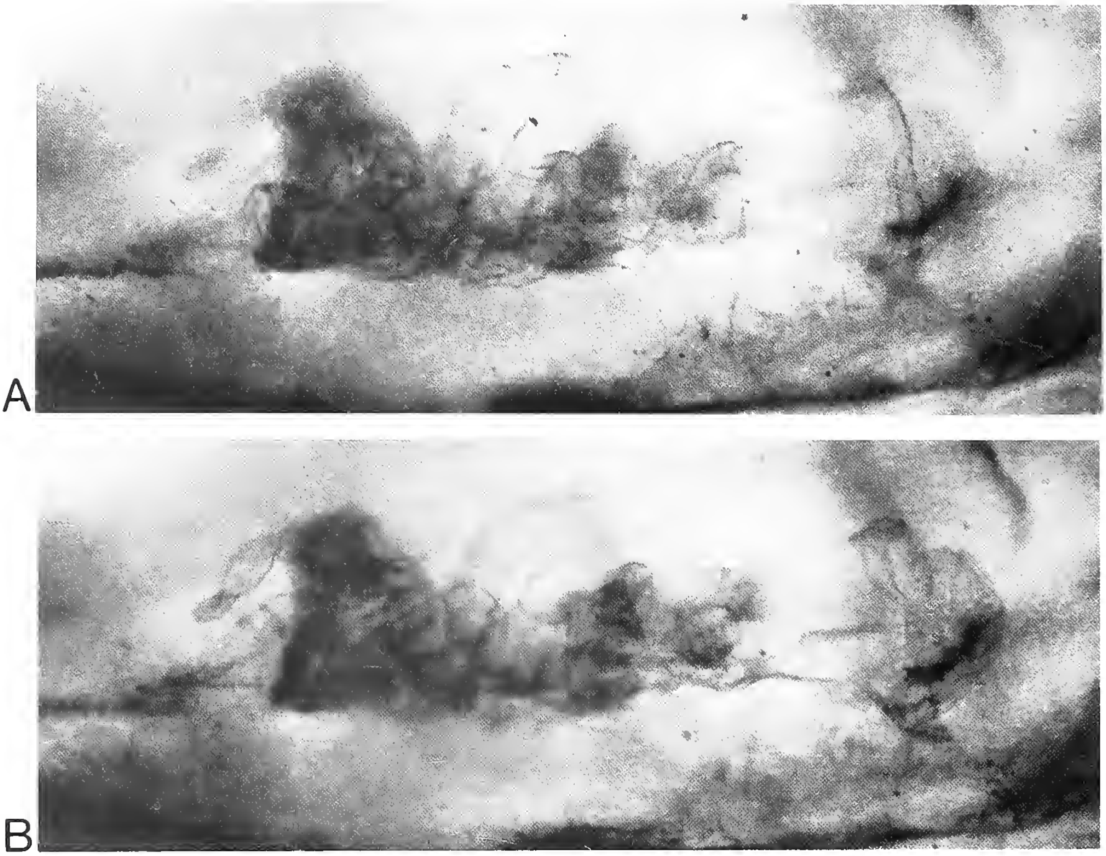
A DEVONIAN age for the oldest known fossil spider was set by Hirst when he described *Palaeocteniza crassipes* Hirst, 1923, from the Pragian Rhynie Chert of Aberdeenshire, Scotland. The description of another fossil assigned to the Araneae, *Archaeometa*? *devonica* Størmer, 1976, from the Emsian of Alken-an-der-Mosel, Germany, added more evidence for the antiquity of the order. The find of a spider spinneret (Shear, Palmer *et al.* 1989) from the Givetian of Gilboa, New York, provided conclusive evidence for the validity of the Devonian as the earliest period in which spider fossils are known to occur. In this paper, results of a re-examination of the Rhynie and Alken spider fossils are presented: the fossils are not spiders, and are reinterpreted as a probable juvenile trigonotarbid and an indeterminate fossil, respectively. The Gilboa spider is placed in a new genus, *Attercopus*, described here. The new genus includes only the animal previously called *Gelasinotarbus? fimbriunguis* (Shear *et al.* 1987), which we now regard as the only known Devonian spider, and the oldest known fossil of the Araneae. In addition, podomeres originally placed in Arachnida *incertae sedis* by Shear *et al.* (1987) are redescribed here, with the addition of new material, as *Ecchosis pulchribothrium* gen. et sp. nov., and placed in Pulmonata *incertae sedis* (it may be an amblypygid), and other arachnid remains from Gilboa are described.

RHYNIE *PALAEOCTENIZA*

In 1923, Hirst described *Palaeocteniza crassipes* as a spider from the Pragian Rhynie Chert of Scotland. James Locke and W.A.S. carried out a detailed photographic study of the specimen (British Museum (Natural History) (BM(NH)) In 24670) in 1987 and 1988. The fossil is in a small chip of chert mounted on a microscope slide. Even if the fossil were to be removed from the slide, no additional views could be obtained, owing to the opacity of the chert behind the specimen. The specimen itself is highly three-dimensional, as are many of the arthropod remains from Rhynie, and thus difficult to photograph. Adding to the problems are the cloudiness of the matrix, opaque inclusions, and the very small size of the specimen, about 0·85 mm long.

In addition to photographs of the whole specimen at low magnifications (Text-fig. 1), a series of about thirty-five optical sections was made at higher magnification, using the very shallow depth-of-field characteristic of Nomarski Differential Interference Contrast (NDIC – see below, *Methods*). These photographs were printed at a large size and each was carefully examined for evidence of

[Palaeontology, Vol. 34, Part 2, 1991, pp. 241–281, 7 pls.]



TEXT-FIG. 1. *Palaeocteniza crassipes* Hirst, 1923. A, B, two views, at different planes of focus, of the holotype (and only known) specimen (BM(NH) In 24670), seen from the left side, anterior to the left, × 130.

spider autapomorphies. In addition, each photograph was traced *seriatim* on a graphics pad and the resultant digitized images were stacked and reconstituted as a rotatable virtual solid using the Jandel computer program PC3D™ (see below, *Methods*). We had hoped that James Locke's efforts to reconstruct the specimen using this program would allow us to examine further details, but this was not to be. The level of resolution attainable was too low, and there were considerable difficulties in digitizing the images, since shallow as the depth-of-field was, at the necessary magnifications subjective judgement was still required as to what was in the plane of focus and what was not, resulting in further blurring of the lines. A careful examination of the specimen itself and of the serial photographs proved to give the most information.

The general condition of the specimen, much crumpled and folded, suggests that it may be a moult. Hirst (1923) noticed a small, thin, scarcely visible object dorsal to the abdomen, which he supposed to be the detached carapace. Since the carapace detaches when arachnids moult, if this identification is correct, its presence and position are further evidence for the specimen being a cast exoskeleton. The prosoma is almost entirely concealed behind the dorsally flexed legs and palps. While the palps appear to be complete, all of the legs on the left side of the specimen (facing the viewer) lack their distal portions. The abdomen is complexly crushed and folded.

Hirst (1923) provided a detailed drawing, which, however, incorporates some errors. The proportions of the right palp are not correct in comparison with the left, to which a segment has been added. In 'restoring' the loose piece of cuticle to its supposed position as carapace, the mass of wrinkles and folds above the leg coxae (perhaps the true carapace) has been omitted, and some of the folds in this structure appear to have been confused with parts of the palps. The second or third left leg has the tibia omitted. In the region of the supposed abdomen, Hirst noted that what had been made in the drawing to resemble spinnerets might be folds of cuticle. This is definitely so; the apparent internal structures of the abdomen are also cuticular folds on the right side of the specimen, seen through the left side.

In attempting to determine the affinity of this fossil, a process of elimination was followed. The general appearance and structure of the body (a prosoma with five pairs of leg-like appendages, and an abdomen attached by a narrowed portion) establishes that it is an arachnid, and that it may belong to the known orders Araneae, Amblypygi, Uropygi, Schizomida, or Trigonotarbida. The presence of leg-like (not raptorial) palps rules out Amblypygi, Uropygi, and Schizomida, at least as they are presently known.

Devonian trigonotarbids differ from potentially contemporaneous spiders in a number of ways. While both groups may have segmented abdomens, trigonotarbids have three tergal plates per segment and lack spinnerets. The eyes of any contemporaneous spiders were likely to have been grouped on a centrally located tubercle, as in the modern mesothele spiders, while those of Devonian palaeocharinid trigonotarbids are dispersed in three groups: a median group of two, and two lateral groups which may consist of several minor and major lenses each (Shear *et al.* 1987). All the Devonian trigonotarbids we have examined have a simple bicondylar hinge joint between the patella and tibia, and spiders have a monocondylar rocking joint in this position.

Close examination of the abdomen of the specimen failed to reveal any evidence for or against segmentation (despite the clear segmental lines in his illustration, Hirst (1923, p. 460) wrote: '…it is impossible to be quite certain whether this [the abdomen] is segmented or not.'). Thus the number of tergites that might be present for each segment cannot be ascertained. The 'spinnerets' have already been alluded to; as Hirst inferred, this is in fact a fold of the abdominal cuticle that can be traced continuously until it merges with other folds of the structure. The entire abdomen was also carefully examined for spinnerets, because we suspected that it might have been twisted through 180°, and because in living mesothele spiders the spinnerets are located about in the middle of the ventral surface of the abdomen, which is supposedly their primitive position. We found no indication whatsoever of spinnerets.

Careful focusing revealed that among the crushed mass of the prosoma was an object that resembles an eye tubercle and seems to bear at least two hemispherical lens-like protrusions. Unfortunately this evidence is inconclusive, because at least two eye lenses would be present on a median tubercle both in trigonotarbids and spiders. The complicated folding and distortion of the carapace and its concealment behind the legs made it impossible for us to find any indication of lateral eye groups.

The patella–tibia articulation can be seen on just one of the legs, probably the left third leg. It may be possible to make out two dorsally situated articular condyles on the distal end of the patella, but at the level of magnification required to see them, the optical properties of the chert interfere significantly.

In summary, the fossil carries none of the autapomorphies of spiders that could be seen on a specimen of this size and level of preservation, but its identity as a trigonotarbid is only suggested (by the possible pattern of patella–tibia articulation). It should be pointed out, however, that scores of trigonotarbids have been seen in the Rhynie chert, and that this specimen is the only one for which a spider identity has been suggested. Our hypothesis is that *Palaeocteniza crassipes* Hirst is a moulted exoskeleton from an early instar trigonotarbid.

ALKEN *ARCHAEOMETA*

One of only four fossil sites with Devonian terrestrial animals, Alken-an-der-Mosel, Germany, has yielded impression fossils of lower Emsian age, including trigonotarbids, scorpions, eurypterids, and arthropleurids (Stormer 1976; Brauckmann 1987). One fossil from this deposit, *Archaeometa?*

devonica Stormer, 1976, was identified as a spider (Stormer 1976). A policy against type-specimen loans at the Senckenberg Museum, which houses this specimen, meant that we were unable to examine the original. However, we were able to study a plaster cast, and the photograph and drawing published by Stormer. The specimen consists of an elongate blob with a few transverse lines at one end and a vaguely indicated region at the other which may be part of some plant remains (Stormer 1976, figs 48 and 49; pl. 5, fig. 2*a*,*b*). Stormer indicated that he had before him Petrunkevitch's drawing of *Archaeometa nephilina* Pocock, 1911, from the Upper Carboniferous of Britain. This drawing (Petrunkevitch 1949, fig. 159) shows a featureless carapace with seven legs radiating from it, and an elongate abdomen with two longitudinal lines and four or five terminal segments.

There are two similar specimens of *A. nephilina* in the British Museum (Natural History) which were examined in 1986 by W.A.S., and subsequently by P.A.S. Specimen In 15863 is the more complete and was the specimen figured by Petrunkevitch. It is relatively poorly preserved and little can be added to the diagrammatic illustration and brief description. Specimen In 31259, the holotype, does not show the transverse 'segmental' lines seen in In 15863. The cuticle is tuberculate and the abdomen bears longitudinal folds; neither of these features are found in contemporaneous spider fossils (e.g. *Eocteniza silvicola*, figured on Pocock's pl. II, fig. 4), but are more reminiscent of other Carboniferous arachnid groups. There are other details visible on this specimen which would reward a detailed restudy. Nevertheless, there are no features which would distinguish either of these specimens as a spider rather than any other arachnid.

In any case, the resemblance of *Archaeometa? devonica* to these two specimens is vague and probably coincidental. There seems to be no reason to consider *Archaeometa? devonica* as a spider or a fossil arachnid of any sort.

THE GILBOA ARACHNIDS

Early reports on the Gilboa fauna (Shear *et al.* 1984) raised the possibility of spiders being among the animals present. The tip of an arachnid walking leg tarsus was illustrated, and diagnosed as being from a spider largely on the basis of serrate ventral setae similar to the silk-handling accessory claws found in some living araneoid spiders. However, in later studies, the possibility of spiders being present receded as it became clear that another related group of arachnids, the Trigonotarbida, dominated the fauna. We were also unable to demonstrate conclusively in the fossils any autapomorphies of spiders. Shear *et al.* (1987), in a detailed study of the trigonotarbids, assigned all pulmonate arachnid fossils from Gilboa to this extinct order, which was placed as the plesiomorphic sister group to the other pulmonate orders. One animal represented only by legs was assigned with some doubt to the trigonotarbid genus *Gelasinotarbus*, and given the species epithet *fimbriunguis*. This name referred to the characteristic claws, set with ventral cuticular fimbriae, not found in any other trigonotarbids. Other characters in these legs, present but undetected in 1987, we now recognize as conclusive evidence of a spider. A single femur with a patch of acute spinules near its base was called Arachnida Incertae sedis B; its cuticle is similar to that of *fimbriunguis*, and other similar femora have now been found in direct connection with pieces of undoubted *fimbriunguis*. A third group of specimens, consisting of podomeres and cuticular fragments, was referred to Arachnida Incertae sedis A. Re-examination of these specimens and of new material with the same distinctive cuticle has produced evidence that they belong to a pulmonate arachnid, close to Amblypygi and Araneae. To complicate matters further, the tarsus illustrated as a possible spider in Shear *et al.* (1984, fig. 1B) is undoubtedly trigonotarbid: it has smooth claws and lacks a tarsal organ.

Late in 1988, conclusive evidence for spiders finally turned up in the Gilboa material: a spinneret (Shear, Palmer *et al.* 1989). This discovery triggered a search for other possible spider parts, and it was soon realized that the spinneret belonged with the legs described in 1987 as *Gelasinotarbus? fimbriunguis*. In addition, some previously unassigned chelicerae and some pieces of carapace belong to this animal.

The 'clasp-knife' form of the chilecera, places it in the Pulmonata (= Arachnidea *sensu* van der Hammen 1977; made up of the orders Trigonotarbida, Uropygi, Schizomida, Amblypygi, and Araneae). Illustrated here for comparison are chelicerae of the uropygid *Mastigoproctus giganteus* (Pl. 7, fig. 5), and the amblypygid *Heterophrynus elaphus* (Pl. 7, fig. 6), and see Shear *et al.* (1987, figs 7, 67, 68) for photographs of trigonotarbid chelicerae. A number of characters unequivoeally place the chelicera in Araneae (see discussion under PHYLOGENETIC RELATIONSHIPS). A cheliceral gland, found only in spiders, is present. The cheliceral fang of *A. fimbriunguis* lacks setae, which are present in all other pulmonates. In all other orders of Pulmonata, the largest cheliceral teeth are at the end of the tooth row opposing the tip of the fang (subchelate condition), while in *A. fimbriunguis*, as in the vast majority of spiders, the largest teeth occur part-way along the row and nearer to the fang articulation than to the fang tip (the subchelate condition occurs in a small number of spiders, but the described arrangement is found only in spiders, among the pulmonates). On the basis of outgroup comparison with, for example, scorpions, the subchelate state is primitive. Thus there are three definite spider synapomorphies present in the chelicera. A significant apomorphy of spiders is the presence of cheliceral venom glands. Whilst the evidence is not entirely certain, in at least two specimens of *A. fimbriunguis* chelicerae there may be a subterminal venom pore near the fang tip (Pl. 1, fig. 7). In addition, as discussed in the detailed descriptions, the articulations present make it clear that the *A. fimbriunguis* chelicera must have been orthognath.

The legs of *A. fimbriunguis* bear numerous lyriform organs; only in spiders are lyriform organs found on podomeres other than the metatarsi.

The pieces of carapace are referred to *A. fimbriunguis* on the basis of their similarity of cuticular patterning.

The evidence that the spinneret, chelicera, legs, and carapace fragments all come from the same morphospecies is overwhelming. All the chelicerae are identical, except for some size differences, and all of the podomere types (trochanter, femur, etc.) are identical within each type. All specimens, including the spinneret and carapace fragments, have the same distinctive cuticular ornamentation, a pattern which appears in no other Gilboa specimens except those that can be unequivocally assigned to the spider on the grounds given above. Finally, the chelicerae and basal leg podomores occur in organic connection on a number of slides. Therefore these Gilboa specimens are considered to belong to the same species, *Attercopus fimbriunguis*.

There are numerous fragments of cuticle among the Gilboa slides which resemble the cuticle of *A. fimbriunguis* at first sight, and which we at first thought could belong to the body of the spider. Some of these were figured by Shear *et al.* (1987) and referred to as Arachnida Incertae sedis A. This animal is characterized by: generally large size; scale-like ornament rather than reticulation; setal sockets which range from small to very large; striated macrosetae and thick, striated, bifid spines (Pl. 7, figs 4 and 8); groups of slit sensilla and lyriform organs; ornamented trichobothrial base on the patella. Minute, *c.* 0·005 mm, circular organs occur on the cuticle surface and appear, at low magnification, similar to the characteristic little slit sensilla of *Attercopus*, but examination at higher magnifications reveals a circular hole rather than a central slit, so they are not the same organ. None of these minute pores bears a seta, and their function is unknown; nevertheless, the difference in morphology from the little slit organs of *Attercopus* gives a useful criterion for distinguishing the two cuticle types. New information on Arachnida Incertae sedis A has been discovered during the present study, and the animal is named *Ecchosis pulchribothrium* gen. et sp. nov., below. The presence of lyriform organs suggests that *E. pulchribothrium* could be a spider, but the distinctive ornamented trichobothrial socket on the patella is puzzling. Virtually identical trichobothrial sockets are found on the living amblypygid *Heterophrynus elaphus* (Pl. 7, fig. 2), but this animal has a quite different leg articulation pattern to that in *E. pulchribothrium*, and a lyriform organ only on the metatarsus. The identity of *E. pulchribothrium* thus remains unclear, but we suggest that it is either an aberrant amblypygid or a member of an extinct, undiagnosed arachnid order.

GEOLOGICAL SETTING

Stratigraphy

The fossils occur in a grey shale in the upper part of the Panther Mountain Formation at a locality on Brown Mountain, Gilboa, Schoharie Co., New York ($7\frac{1}{2}'$ quadrangle sheet 6168 IV NW 1945, approx. 271272 m N by 142951 m E; Banks *et al.* 1985). Further locality details can be found in Banks *et al.* (1972). The original site has now been destroyed to make way for a pump-storage power plant associated with Schoharie Reservoir, but much of the fossil-bearing shale was removed to the Department of Biology, State University of New York at Binghamton, for later processing. The Panther Mountain Formation is part of the Hamilton Group, upper Middle Devonian Erian Series, and is equivalent to the middle Givetian of Europe.

Palaeoecology

Detailed discussion of the taphonomy and palaeoecology of the biota is given in Shear (1986), Shear *et al.* (1987) and Shear and Bonamo (1988). The Gilboa lithology is a dark grey mudstone. The fauna occurs in close association with mats of interlocking spiny stems of the lycopod *Leclercqia*. Consideration of the manner of preservation of the plants suggested to Banks *et al.* (1985) that they were buried *in situ* by low-energy flood waters. Shear *et al.* (1984) suggested that the animals, which were living at the site or may have been carried in by the flow, came to rest by the localized reduction of velocity created by the mesh of *Leclercqia*. the 'natural sieve' effect would exclude large pieces of arthropod cuticle, while the most minute particles could have passed through.

Almost all the arthropods recovered from the Gilboa site were undoubtedly terrestrial. The only exception to this is the occurrence of eurypterid fragments. In the Devonian, these animals lived in both marine and freshwater aquatic habitats, and some were amphibious (Selden 1984, 1985), so their presence in the Gilboa mudstones is not problematical. In addition to the external evidence of sedimentology and associated land flora for the habitat of the arthropods, palaeophysiology provides further proof of their terrestriality (Selden and Jeram 1989). Trichobothria are fine hairs sensitive to high-frequency vibrations, and could only function in air. They occur on the Gilboa pulmonates *Gelasinotarbus bonamoae*, *G. bifidus* (Shear *et al.* 1987, figs 105–120), and *Ecchosis pulchribothrium* (see below), and the pseudoscorpion (Shear, Schawaller and Bonamo 1989). Book-lungs for air breathing occur in the trigonotarbids of Gilboa (Shear *et al.* 1987). While we have no evidence of trichobothria or book-lungs in the Gilboa spider *Attercopus*, all living spiders are terrestrial apart from the secondarily aquatic *Argyroneta aquatica*, found in fresh waters of Europe, and the littoral, southern hemisphere Desidae. The phylogenetic discussion (below) indicates that if *Attercopus* were aquatic, it would also have been secondarily so, since all other Pulmonata are primarily terrestrial.

MATERIAL AND METHODS

Preservation

The animal fossils are preserved as minute, undistinguished, brown to black flakes, which are unrecognizable as animals when in the rock and under incident light microscopy, but transmitted light reveals their zoological nature. The cuticle appears brown in transmitted light, and the depth of colouration is directly correlated with the thickness of the cuticle (or the number of layers of cuticle superimposed in the specimen). The chemical composition of the cuticle is not known; the brown colouration suggests it is organic, but the reduction of much of the plant material in the same beds to carbon indicates the likelihood that the arthropod cuticle has also been altered, probably by repolymerization of the organic molecules, during diagenesis. The arthropods are strongly compressed, necessitating the use of special techniques, such as NDIC, to separate overlapping layers of cuticle. For the same reason, scanning electron microscopy (SEM) is virtually useless for the study of these fossils, revealing only surface features: both original structures and diagenetic effects.

The fossils are fragmentary; only rarely are podomeres and other parts found in organic connection with others. However, the occurrence of such specimens is vital for the correct identification of loose podomeres and reconstruction of the animals. The dearth of pieces of carapace and abdomen of the arachnids can be explained by the fact that podomeres have two surfaces, so that when compressed together they remain coherent and are less likely to fragment than the body parts which consist of a single sheet of cuticle. The carapace and abdomen cuticle is represented by the many 'scraps' which occur on the slides. The nearly complete trigonotarbid carapaces and abdomens described by Shear *et al.* (1987) are rare, and mostly consist of both left and right (or dorsal and ventral) surfaces compressed together.

Further discussion of the preservation of the Gilboa fauna is given in Shear *et al.* (1987).

Methods

The specimens were recovered from the rock matrix by digestion in concentrated hydrofluoric and hydrochloric acids (see Shear *et al.* 1987; Shear and Bonamo 1988, for details). After washing in distilled water, the animal fossils were separated from the abundant plant fragments, as far as possible, and mounted in CMC or Clearcol on plain microscope slides. The preparation was done in the laboratory of P.M.B. in Binghamton, and the prepared slides were then sent to Hampden-Sydney for study by P.A.S. and W.A.S.

The slides were studied using an Olympus Vanox II biological microscope with a Nomarski Differential Interference Contrast (NDIC) facility. This illumination is particularly useful at high magnification and for the optical separation of closely adpressed layers of cuticle. Use was made of an Olympus SZH stereomicroscope for low magnification work, particularly on comparative extant material; for photography, this was cleared of muscles by soaking overnight in a solution of potassium hydroxide. Camera lucida attachments to both microscopes facilitated accurate drawing of the specimens, and photographs were taken on 35 mm Kodak Technical Pan film at ASA 50 with Olympus PM10 cameras mounted on these instruments. On plates and text-figures, unless stated otherwise, all photographs were taken in transmitted light with NDIC on the Vanox.

The computer program Jandel PC3D™ (available from Jandel Scientific, 2526 Bridgeway, Sausalito, California 94965, USA) was used for the three-dimensional reconstruction of *Palaeocteniza crassipes*, and the program MacClade 2.1 (Maddison and Maddison 1987) was extremely useful in the phylogenetic analysis.

Abbreviations and conventions used in text-figures are as follows: a, anterior, antero-; ar, articulation; ch, chelicera(l); cl, claw; co cx, costa coxalis; cu, cuticle; Cx, coxa; d, dorsal; di, distal; e, edge; f, fold; Fe, femur; gl, gland; i, inferior, infero-; m, arthrodial membrane; ma, marginal; me, median; ms, macroseta; Mt, metatarsus; p, posterior, postero-; pa sp, palpal spinules; Pa, patella; pd, paired; po, poison duct opening; pr, proximal; ps, prosoma; r, ridge; s, superior, supero-; sc, sclerite; sl, slit sensilla; sr, serrated; st, sternum, su, surface; t b, trichobothrial base; Ta, tarsus; ta or, tarsal organ; Ti, tibia; Tr, trochanter; tv, transverse; v, ventral; X, artefact.

Unless stated otherwise in the legend to camera lucida drawings: dashed lines show linear features showing through cuticle from behind; finely dotted areas are internal surfaces; coarse dots show arthrodial membrane; setal sockets and slit sensilla (where shown) are infilled in black when on surfaces showing through from behind; prominent spores (where shown) are in black.

Repository and authorship

Type and figured material is deposited in the Department of Invertebrates, American Museum of Natural History, New York (numbers prefixed AMNH), but are referred to in the text by their slide numbers. Most slide numbers consist of a series number (the first two numbers, e.g. 411.7, or the first only if only two numbers are present, e.g. 329), followed by the number of the slide within the series. The last, slide, number is prefixed with the letters AR (or Ar) on the slide itself, and quoted thus in earlier publications; these letters are omitted here for brevity. The slide may include more than one specimen, commonly of a different arthropod, but quoting the slide number makes retrieval of specimens for future study easier, facilitates references to earlier papers on the Gilboa

TABLE 1. List of specimens mentioned in text.

Slide No.	AMNH No.	Illustration	Brief description
Attercopus fimbriunguis			
329.1	43162	Pl. 3, fig. 4; Text-fig. 6D	palpal femur + patella
329.3	43163	Pl. 3, fig. 2; Text-fig. 6B	femur
329.3	43163	Pl. 4, fig. 1; Text-fig. 7A	distal tibia
329.3	43163	Pl. 4, fig. 10; Text-fig. 7F	metatarsus
329.38	43168	Pl. 4, fig. 8	metatarsus
329.39	43098	Text-fig. 12B	patella
329.53	43099	Pl. 4, fig. 9	tibia
329.57	43100	Text-fig. 12F	metatarsus
329.58	43101	Shear *et al.* 1987, fig. 134	HOLOTYPE, metatarsus, tarsus
329.59	43102	Pl. 3, fig. 3; Text-fig. 6C	distal femur + patella
329.59	43102	Text-fig. 12C	trochanter
329.69	43106	Pl. 2, fig. 5; Text-fig. 5E	various; femur, patella, tibia
329.69	43106	Pl. 6, fig. 5; Text-fig. 9D	palpal tarsus
329.70	43107	Text-fig. 12A	PARATYPE, femur + patella
329.70	43107	Text-fig. 12D, E	2 metatarsi, proximal tarsus
329.16.34	43164	Pl. 5, fig. 2	tarsus
329.22.9	43165	Pl. 1, fig. 7; Text-fig. 4E	chelicera
329.31*a*.M1	43166	Pl. 3, fig. 7; Text-fig. 6E	various; femur + patella
329.31*a*.M2	43047	Pl. 6, fig. 4	legs
334.1*a*.4	43170	Pl. 5, figs 1 and 3; Text-figs 8A–C	2 legs, patella to tarsus
334.1*a*.6	43171	Pl. 2, fig. 4; Text-fig. 5D	femur
334.1*a*.7	43172	Pl. 1, figs 6 and 8; Text-fig. 4C	chelicera
334.1*a*.8	43173	Pl. 4, figs 6; Text-fig. 7E	tibia
334.1*a*.9	43174	Pl. 2, fig. 1; Text-fig. 5A	femur
334.1*b*.12	43175	Pl. 3, fig. 5; Text-fig. 6G	distal femur + patella
334.1*b*.34	43176	Text-figs 10, and 11A, B, C	spinneret
334.1*b*.38	43177	Pl. 5, fig. 5; Text-fig. 8D	tarsus
334.1*b*.86	43178	Pl. 3, fig. 6; Text-fig. 6F	femur + patella
411.02.12M.6	43179	Pl. 6, figs 1 and 2; Text-fig. 9A	metatarsus + tarsus
411.7.19	43052		PARATYPE, femur
411.7.33	43180	Pl. 1, figs 4 and 5; Text-fig. 4D	chelicera
411.7.45	43181	Pl. 4, fig. 3; Text-fig. 7C	distal tibia
411.19.83	43182	Pl. 2, fig. 2; Text-fig. 5B	coxa
411.19.98	43183	Pl. 4, fig. 7; Text-fig. 7G	distal tibia
411.19.102	43184	Pl. 2, fig. 7; Text-fig. 5H	3 coxae, 1 trochanter
411.19.243	43185	Pl. 3, fig. 8	proximal femur
411.19.248	43186	Pl. 4, fig. 5; Text-fig. 7D	patella
411.19.250	43187	Pl. 2, fig. 8; Text-fig. 5G	coxa
411.19.251	43188	Pl. 4, fig. 11	metatarsus
411.20.25	43189	Pl. 4, fig. 2; Text-fig. 7B	patella
2002.12.49	43190	Pl. 4, fig. 4	tibia
2002.12.79	43191	Pl. 3, fig. 1; Text-fig. 6A	femur
2002.12.90	43192	Pl. 1, figs 2 and 3; Text-fig. 4B	cheliceral teeth
2002.12.102	43193	Pl. 1, fig. 1; Text-fig. 4A	anterior carapace
Ecchosis pulchribothrium			
411.1.33	43194	Pl. 7, fig. 1	PARATYPE, distal femur
411.7.37	43195	Pl. 6, fig. 6; Text-fig. 9B	HOLOTYPE, patella + prox. tibia
411.7.86	43111	Shear *et al.* 1987, figs 149 and 150	PARATYPE, distal patella
411.19.96	43198	Pl. 6, fig. 3; Text-fig. 9C	patella
411.19.137	43169	Pl. 7, fig. 4	large, bifid spine
411.19.184	43195	Pl. 7, fig. 3	lyriform organ
411.19.188	43196	Pl. 7, fig. 8	PARATYPE, probable tibia
411.19.206	43197	Pl. 7, fig. 7	sheet of cuticle
2002.9.13	43097	Pl. 2, fig. 3; Text-fig. 5C	coxa
Arachnida *incertae sedis*			
334.1*a*.4	43198	Pl. 5, Fig. 3	flagelliform appendage
2002.9.20	43199	Pl. 5, Fig. 4	flagelliform appendage

fauna in which slide numbers are used, and locates the specimen to the original rock sample. Thus it will be possible in the future to collate data on the whole Gilboa biota to a fine degree of accuracy. Table 1 lists the described specimens both by their AMNH accession number and the slide number. A complete list of the microscope slides which bear fragments of *Attercopus fimbriunguis*, *Ecchosis pulchribothrium*, and Arachnida *incertae sedis* is deposited as Supplementary Publication No. SUP 14040, 5 pp., at the British Library, Boston Spa, Wetherby, Yorkshire LS23 7BQ, England. Copies of this can be obtained by writing to the British Library at the above address, enclosing prepaid coupons available from most libraries throughout the world.

In addition to the fossils, the following material (both males and females, and from the W. A. Shear Collection, unless otherwise stated) of extant arachnids was studied for comparative purposes: Araneae: *Liphistius sumatranus* Thorell, Sumatra, American Museum of Natural History collection; Amblypygi: *Heterophrynus elaphus* Pocock, Ecuador; Uropygi: *Mastigoproctus giganteus* (Lucas), Florida; Schizomida: species indet., Mexico.

Following previous practice (Shear *et al.* 1987), authorship of new taxa is attributed to Selden and Shear. Bonamo discovered and supervised the preparation of the Gilboa material; Selden and Shear are responsible for other information and ideas in this paper.

RECONSTRUCTION OF THE GENERALIZED LEG OF *ATTERCOPUS*

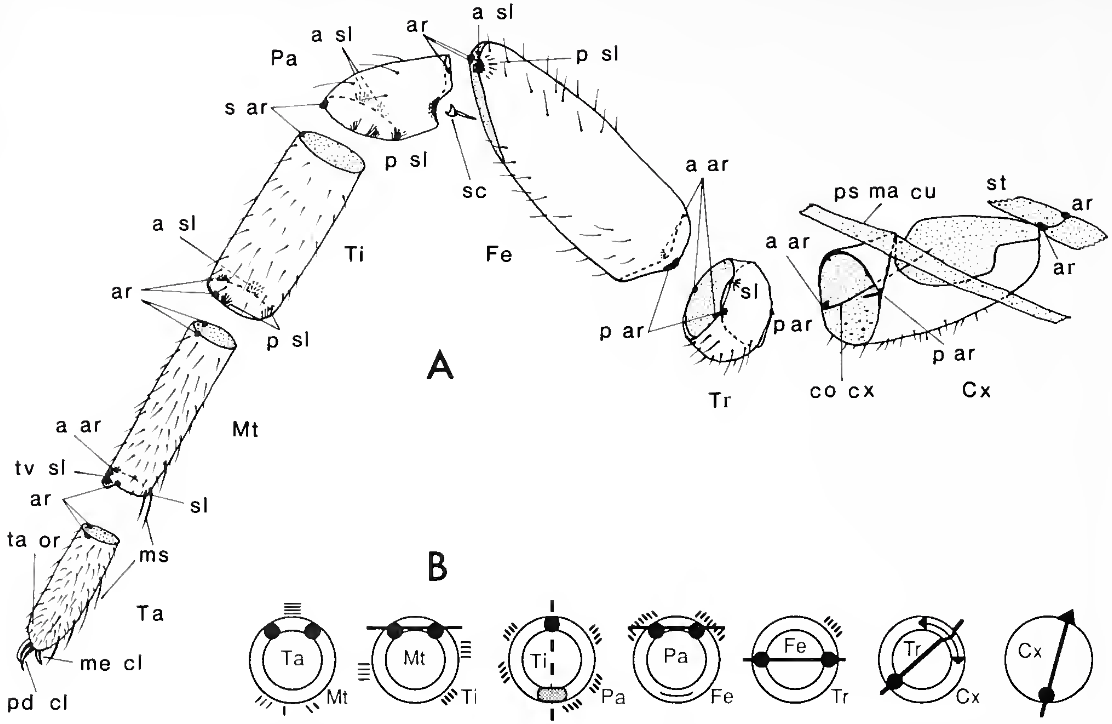
The reconstruction (Text-fig. 2) reflects a combination of the known morphology of various legs, some of which are suspected to be leg 1 by their close relationship with palpal femora and chelicerae, but for most specimens the leg to which they belong is not known. The reconstruction is to be used as a key to interpretation of the fossils, and for comparative purposes in a general sense. However, it must be remembered that no one leg of *Attercopus fimbriunguis* looked exactly like this reconstruction, and in particular, the relative proportions of the podomeres would have varied between legs.

There are a number of ways in which the orientation of podomores can be inferred. Inferior and superior are fairly straightforward: comparison of the articulation points with those of living spiders, together with a consideration of the way the leg has to work as a functional unit, is normally sufficient. Assessing which is anterior and which posterior is less easy. The trochanter can be oriented by observing its relationship to the coxa, the orientation of which is known because of the asymmetry in the joint and comparison with extant arachnids. However, there are no trochanters connected to femora which are sufficiently well preserved to enable the following of the orientation down the leg. Since most joints beyond the coxa are symmetrical, their morphology is of little use in orientation, but there is an asymmetrical distribution of slit sensilla and lyriform organs around the distal joints of podomeres. The palpal femur bears a patch of spinules in an inferior position, to one side of its sagittal plane. The function of these spinules is not known, but we are assuming that, whatever their function (see below), they are most likely to occur on the anterior side of the podomere. Therefore, the palpal femur can be oriented, and since this podomere is attached to a patella, this podomere can also, and so on down the leg. A further logical step is required in the assumption that the apparent similar distribution of slit sensilla on palpal podomeres and on the podomeres of other legs reflects a real serial homology. These assumptions have only been made in order to provide an orientation for the reconstructed generalized leg, and not for any other purpose. Should the orientation prove to be incorrect, then the references to anterior and posterior would simply require reversal.

PHYLOGENETIC RELATIONSHIPS OF *ATTERCOPUS FIMBRIUNGUS*

Cladistic analysis

Characters and character states used in the analysis are listed in Table 2, the data matrix is given in Table 3, and the cladogram in Text-figure 3. The tree was rooted by arbitrarily including an ancestor plesiomorphic for all characters.



TEXT-FIG. 2. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). A, reconstruction of a typical walking leg, posterior aspect. B, diagrammatic representation of walking leg joints, distalmost to the left; each joint is viewed from the distal direction with the anterior to the left, the inner circle representing the distal podomere, the outer the proximal podomere; solid circles are articulation points and straight lines are articulation axes, short lines represent slit sensilla. The body–coxa joint is highly diagrammatic; the lower articulation representing the coxosternal attachment, the upper triangle representing the attachment of the coxa to the prosomal marginal cuticle. The upper coxa–trochanter articulation is a movable sclerite set in the arthrodial membrane, which allows rocking. Slit sensilla omitted from coxal distal joint. The trochanter–femur joint is a horizontal pivot. The femur–patella joint is a superior bicondylar hinge, and there is a sclerite embedded in the inferior arthrodial membrane. The patella–tibia joint has a superior articulation, but a close connection of the podomeres inferiorly allows the joint to work as a loose vertical pivot. The tibia–metatarsus joint is a superior bicondylar pivot. The metatarsus–tarsus joint bears antero- and posterosuperior articulations forming a superior bicondylar hinge, but the joint may be uncoupled on relaxation of the muscles, allowing rocking.

Shear *et al.* (1987) presented a cladistic analysis based on 23 of the same characters as used here. The additional characters accommodate the division of the Araneae into *Attercopus*, Mesothelae, Mygalomorphae, and Araneomorphae. If a character is not discussed below, the discussion will be found in the 1987 paper. Some of the previously used 23 characters have been re-evaluated; in the following discussion, the character number given is from Table 2, and the character number from Shear *et al.* (1987) is in brackets.

Original characters. Character 8 [5] has been recoded. Further investigation of the patella–tibia articulation demonstrated that the joint in living spiders has an additional specialization, compression zone Y (CZY, see later), not present in *Attercopus*. Further, while the joint is immobilized (fixed) in Amblypygi, considerable movement is possible at that articulation in legs 2–4 of Uropygi and Schizomida (in leg 1 the patella and tibia are entirely fused without trace of a suture). We do not know if the condition on the more posterior legs of Uropygi and Schizomida represents a reversal or the retention of a primitive condition, but we decided to code it as a primitive retention on the grounds of parsimony. Character 9 [16] has also been recoded, because an

TABLE 2. Characters and character states used in the phylogenetic analysis.

Characters	Plesiomorphic state	Apomorphic state
1. cheliceral segmentation	3-segmented	2-segmented
2. plagula ventralis	absent	present
3. book-lungs	absent	present
4. sperm flagellum	9+2	9+3
5. segment 7	broad	narrowed
6. eggs	not protected	protected by secretions
7. lateral eyes	minor lenses present	minor lenses absent
8. Pa-Ti joint	bicondylar hinge	1, rocking, no CZY 2, rocking with CZY 3, immovable
9. labium	absent	present
10. grouped slits/lyriforms	absent	present
11. tarsal organ	absent	present
12. cheliceral poison gland	absent	present
13. silk glands	absent	present
14. tibial lyriforms	absent	present
15. cheliceral fang	setose	naked
16. cheliceral gland	absent	present
17. male palp	unmodified	modified
18. abdominal segments	visible	hidden
19. tartipores	absent	present
20. sternum	broad, unitary	reduced, divided
21. palps	leg-like	raptorial
22. leg 1	leg-like	antenniform
23. posterior sucking stomach	present	absent
24. abdominal flagellum	absent	present
25. palp coxae	free	fused
26. postabdomen	2-segmented	3-segmented
27. abdominal tergites	entire	divided
28. fimbriae on claws	absent	present
29. spinules on palpal Fe	absent	present
30. Ti-Mt organ	absent	present
31. clavate trichobothria	absent	present
32. anterior media spinnerets	absent	1, present 2, lost
33. chelicerae	orthognath	labidognath
34. cleaning brush on palp	absent	present
35. anal glands	absent	present
36. male flagellum	unmodified	modified
37. central nervous system	partly in abdomen	wholly in prosoma
38. trichobothria	present	absent

examination of specimens has convinced us that a labium (sternite of the palpal segment modified as a lower lip) does not in fact occur in Amblypygi, Uropygi, and Schizomida. In amblypygids, a long projection goes forward from the sternite of the first leg, but could not function as a labium. In uropygids and schizomids, the palpal sternum is an immovable pentagonal sclerite and the ventral wall of the preoral cavity (camerostome) is formed by the fused palpal coxae. Character 5, the narrowing of segment 7, has replaced [18]: presence or absence of a pedicel. We think that the key feature here is the reduction in width of that segment, which occurs to a greater (Araneae, Amblypygi) or lesser (Trionotarbida, Uropygi, Schizomida) degree in all of the taxa involved.

TABLE 3. Data matrix used in the phylogenetic analysis. 0 = plesiomorphic state, 1 = apomorphic state, 2, 3 = alternative apomorphic states, ? = character state uncertain. See text for details.

		1		2		3		
Characters	12345	67890	12345	67890	12345	67890	12345	678
Trigonotarbida	111?1	?0000	00000	00000	00?00	01000	00000	0?1
Attercopus	111??	??1?1	11111	1??0?	00??0	??110	0?000	0?1
Mesothelae	11111	11211	11111	11000	00000	00001	11000	010
Mygalomorphae	11111	11211	11111	11110	00000	00000	02000	010
Araneomorphae	11111	11211	11111	11110	00000	00000	01100	010
Amblypygi	11111	11301	10000	00001	11000	00000	00010	010
Uropygi	11111	11101	10000	00001	11111	10000	00001	000
Schizomida	11111	11101	10000	00001	11111	10000	00000	100

New characters. Characters 10 and 14: slit sensilla are unique to chelicerates. We have assumed that the primitive arrangement was scattered, single slits on most or all body surfaces, and these still occur in all arachnids. However, the slits, which function as cuticular strain gauges, are found in greater numbers near articulations or points where the cuticle is likely to be stressed (Barth 1978, 1985). This has led in turn to the formation of loosely organized groups of slits, and thence to tightly coupled, parallel slits, commonly surrounded by a cuticular border, known as lyriform organs. In true lyriform organs the slit sensilla are neurally integrated to act as a single organ; this integration is recognized morphologically where the slits are as close together as their individual widths, and are parallel to each other. They may change in length gradually across the organ, giving the appearance of the arrangement of strings in a lyre or harp. A multiplicity of lyriforms is clearly apomorphic, and in character 14, the presence of lyriforms on the leg tibiae stands in for this increase in their number. In trigonotarbids, we have not detected grouped slits or lyiforms, though large slits occur in greater numbers near the distal ends of podomeres (see Shear *et al.* 1987, figs 11, 46, 79–81). Lyriforms occur in amblypygids and uropygids only on the distal ends of the metatarsi of legs 2–4, and are oriented parallel to the long axis of the leg; spiders have this metatarsal lyriform, which is oriented perpendicular to the long axis of the leg, as well as many additional lyriforms on other podomeres which are oriented parallel to the long axis (Barth 1985; Barth and Stagl 1976; Moro and Bali 1986).

Character 11: typical tarsal organs (Blumenthal 1935; Forster 1980) occur on the walking leg tarsi of all living Pulmonata (Amblypygi and spiders, Forster 1980, and pers. obs.; antenniform legs of Amblypygi, Foelix *et al.* 1975 ('pit organ'); walking legs of Uropygi, pers. obs. and R. Forster, pers. comm.; walking legs of Schizomida, pers. obs. and R. Forster, pers. comm.). We have not detected this organ on the tarsi of trigonotarbids, but it is present in *Attercopus*. While similar structures are found on the tarsi of scorpions and ticks (Foelix and Axtell 1972; Foelix and Schabronath 1983), they appear ultrastructurally different and their homology has not been established. Thus the presence of the tarsal organ is treated here as a synapomorphy for the orders of Pulmonata excepting Trigonotarbida, though it may later be shown to be more widespread in Arachnida.

Character 15: a naked cheliceral fang is apomorphic by comparison with the setose condition of the palp and walking legs, with which the chelicera is serially homologous. Among the Pulmonata, a naked cheliceral fang is found only in spiders, all other pulmonate orders have a brush of setae on the fang (see, for example, Pl. 7, figs 5 and 6; Shear *et al.* (1987) figs 7, 67, 68).

Character 16: the cheliceral gland described by Forster and Platnick (1984) has been reported only in spiders; it has been found in all species so far examined from a wide selection of families (R. Forster, pers. comm.). Raymond Forster (pers. comm.) stated that he has found a series of scattered pores near the midpoint of the ventral surface of the chelicera in amblypygids, which he considers a cheliceral gland. Using light microscopy (including oil immersion examination of cleared cuticle) we were not able to confirm these observations, but a purposeful search for the gland may reveal it in orders other than Araneae. In pseudoscorpions, glands also open on the chelicera (Vachon 1966), but they are very distinct in appearance and probably not homologous. We propose the presence of this distinctive gland is yet another autapomorphy for the order Araneae.

Character 18: in opisthothele spiders, the segmentation of the abdomen is suppressed and is either entirely concealed from external view, or revealed only on the maturity of males of a few species of mygalomorphs, and even then only in the anterior part. This is a synapomorphy for Mygalomorphae and Araneomorphae.

Character 19: tartipores – these peculiar structures, like small, collapsed pastries (hence the name), evidently mark the position of spigots on the spinnerets in previous instars (Kovoor 1986; Coddington 1989). They do not occur in *Attercopus* nor in mesotheles (pers. obs. on *Liphistius sumatranus* and *L. malayanus*). The number of spigots on spider spinnerets increases with each instar; in mesotheles the increase is accomplished by adding more pseudosegments to the spinneret. We consider this mechanism primitive, and the presence of tartipores synapomorphic for mygalomorph and araneomorph spiders.

Character 26: a two-segmented postabdomen is present in trigonotarbids, spiders, and amblypygids. Counting segments shows that uropygids and schizomids have added a third, basal segment (probably by the narrowing of the segment just in front of the primitive two-segmented postabdomen), which we consider a synapomorphy for that group, correlated with the postanal abdominal flagellum.

Characters 28 and 29: fimbriate claws and palpal femoral spinules are autapomorphies of *Attercopus*, by outgroup comparison and the criterion of 'special structures'.

Characters 30 and 31: a highly specialized organ for detecting deflection of the metarsus with respect to the tibia is present among spiders only in living mesotheles (Platnick and Goloboff 1985). Likewise, special club-shaped trichobothria (Foelix 1985) are unique to this group (Platnick and Goloboff 1985).

Character 32: by outgroup comparison, the loss of the anterior median spinnerets is autapomorphic for mygalomorph spiders. We might add here that there are other spinneret and spigot characters that may prove useful for phylogenetic analysis among spiders; some of these have already been described by Coddington (1989) and others are under study by J. M. Palmer and J. A. Coddington.

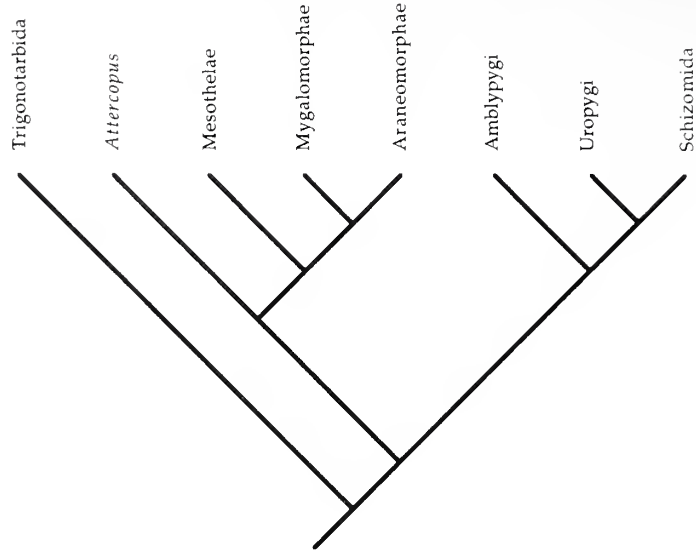
Character 33: labidognath chelicerae are found only in araneomorph spiders and are autapomorphic for that group.

Character 38: the distribution of trichobothria in the Arachnida has been discussed by Kaestner (1968), and Reissland and Görner (1985). They are found in spiders, amblypygids, uropygids, schizomids, palpigrades, scorpions, pseudoscorpions, and mites, but not in solifuges, ricinuleids, or opilionids. Their occurrence in scorpions and palpigrades, both considered primitive arachnids, and their general appearance elsewhere argues for considering their absence in any arachnid a loss. We have not found trichobothria in trigonotarbids, nor in *Attercopus*. Shear *et al.* (1987) described trichobothria in the supposed trigonotarbid *Gelasinotarbus bonamoae*, but new studies of this animal have convinced us that it is not, after all, a trigonotarbid, nor does it seem to be a spider. The loss of trichobothria is thus proposed as another autapomorphy for Trigonotarbida.

We are more concerned about the complete lack of trichobothria encountered during our high-magnification studies of well-preserved podomeres of *Attercopus*. We have found no mention in the literature of spiders without trichobothria, and R. Forster and N. Platnick, who have surveyed hundreds of species using SEM, reported that they have found no spiders which lack these sense organs (R. Forster, pers. comm.). Had we not found tarsal organs and longitudinally oriented lyriforms on *Attercopus* podomores, as well as having been able to match their cuticle to that of the isolated spinneret, we would question our assignment of these fossils to Araneae. We must regard the loss of trichobothria in *Attercopus* as an autapomorphy independent of their loss in trigonotarbids.

Cladogram. Using these 38 characters, we have produced a 36-step cladogram (Text-fig. 3) with a consistency index of 0·97.

In an earlier, preliminary report on the spinneret of *Attercopus fimbriunguis*, Shear, Palmer *et al.* (1989), were able to narrow down the number of possible cladograms for spider sub- and infra-orders to three, arguing as follows. Recent views of spider evolution divide the Order Araneae into two suborders. Suborder Mesothelae includes a small number of species today restricted to southeast Asia, Indonesia, and Japan; they are united by a number of synapomorphies, including a peculiar sense organ between the tibiae and metatarsi of the legs (see above). Mesotheles are better known to arachnologists for their primitive characters, including an externally segmented abdomen and the possession of eight (rarely seven) spinnerets, which are located not at the end of the abdomen, but near the middle of its ventral surface. Suborder Opisthothelae includes all other spiders, in which the number of spinnerets has been reduced to six, four, or two and moved to the posterior end of the abdomen, which is not externally segmented. Within this group, Mygalomorphae ('tarantulas' in the North American sense) have lost all vestiges of the anterior median spinnerets, while Araneomorphae carry a cribellum (repeatedly lost in many lines)



TEXT-FIG. 3. Cladogram of relationships between *Attercopus* gen. nov., infraorders of Araneae, and orders of Pulmonata, as inferred by the cladistic analysis (see text for details). The cladogram has a length of 36 and a consistency index of 0·97.

homologous to the anterior median spinnerets of mesotheles, and have chelicerae rotated to the labidognath position, so that the fangs point toward one another.

The spinneret is described in detail below. Using information from the description, Shear, Palmer *et al.* (1989) were sure the spinneret could not have come from the living clade of mesotheles, because in mesotheles the large lateral spinnerets of each pair are pseudosegmented, with spigots in ranks of 2, 3, or 4 on the mesal surface of a pseudosegmental ring, and the smaller, single-articled median ones bear only a single spigot. Because the Devonian spinneret is not pseudosegmented, yet bears more than one spigot, it could not have come from a mesothele spider similar to those living today.

Araneomorph spiders are ruled out because the spigots of their spinnerets are strongly differentiated from one another and from those of mygalomorph spiders in characteristic ways, and all spigots on the fossil specimen are of the same size and shape.

Mygalomorph spiders have single-articled posterior median spinnerets with numerous spigots arranged as they are in the fossil. The presence of undifferentiated, or only weakly differentiated, spigots that are more densely clustered near the tip of the spinneret is consistent with mygalomorph spider posterior median spinneret anatomy. However, both mygalomorph and araneomorph spinnerets have peculiar nipple-shaped structures called tartipores (see above), which represent the positions of spigots in previous instars. Tartipores are not present on the Devonian spinneret. In addition, mygalomorph spinnerets usually have two types of spigots present.

Finally, the form of the spigots themselves does not, in detail, agree with that of mygalomorph spigots. Mygalomorph spigots usually have an articulated shaft, which joins the base by means of a well-defined, sleeve-like fold. At least the distal third of the shaft has sculpture. However, the rastelloid clade of mygalomorphs have non-articulated shafts and extremely fine sculpture, visible only when viewed with the SEM. Diagenetic changes in the fossil spinneret may have made it impossible to resolve such fine detail as the distal shaft sculpture.

Mesothele spigots, on the other hand, are uniform in morphology, with a broad, conical base and a long, gradually tapering, unsculptured distal shaft that merges smoothly into the base. The spigots of the fossil are of this type. Considering the absence of tartipores, of a sleeve-like fold at the base of the spigot shaft, and the likelihood that distal sculpture is absent, the spigots are more like mesothele spigots than mygalomorph ones.

Therefore, the combinations of apomorphies found in the three living clades would seem to exclude the fossil from all of them. The problem then becomes placement of the fossil as a sister group of one, two or all of these clades. The presently accepted 3-taxon statement for the groups of spiders so far discussed is: Mesothelae (Mygalomorphae (Araneomorphae)). The fossil spinneret is probably not from a spider belonging to the sister group of either Araneomorphae or Mygalomorphae, because to place it in either of those positions would require the *ad hoc* secondary loss of tartipores in the fossil clade. Thus, either *Attercopus fimbriunguis* would prove to be the sister group of all other spiders, of only mesotheles, or of opisthotheles, leaving a basal trichotomy in the cladogram of spider suborders. Shear, Palmer *et al.* (1989) ended their argument at this point, because additional *Attercopus* fragments had not yet been identified, and no characters were available to resolve the trichotomy.

Careful examination of the legs of *A. fimbriunguis* has provided evidence that the trichotomy can be resolved in favour of this Devonian clade as the sister group of all other spiders. This evidence comes from the structure of the patella–tibia joint, which, as we (Shear *et al.* 1987) and others (Manton 1977; van der Hammen 1977, 1985, 1986; Shultz 1989) have shown, is of great phylogenetic significance.

In trigonotarbids, this joint is a simple bicondylar hinge, probably the plesiomorphic form at least for Pulmonata (Shear *et al.* 1987). In the other pulmonate orders, it becomes a specialized rocking joint, with a single dorsal condyle and held together with strong muscles. In spiders, three lyriform organs are found on the posterior surface and two on the anterior, and this rich array of proprioceptors is associated with the complex movement of this joint in more than one plane (Manton 1977). The additional complex mobility of the patella–tibia joint is conferred at least in part by a posterior emargination, occupied by lightly sclerotized cuticle and extending proximally from the distal edge, which Manton called 'compression zone Y' (CZY). The presence of CZY pushes the middle lyriform of the three posterior ones almost to the proximal edge of the podomere. However, in amblypygids, this joint, while retaining vestiges of the rocking articulation, is nearly immobile. In uropygids and schizomids the first leg patellae and tibiae are entirely fused and no separate patella appears. On the walking legs (2–4) the joint is movable, but, as discussed above, we are not certain if this mobility is primary or secondary.

The condition of this joint in *A. fimbriunguis* is of great interest; the rocking articulation is present but CZY is absent. Functionally, this suggests substantially less mobility at this joint than in other spiders, but more than in trigonotarbids.

It is suggested that the common ancestor of Araneae and the 'pedipalp' orders (Uropygi, Amblypygi, Schizomida) had the type of joint found in *A. fimbriunguis*, which is still present in Uropygi and 'locked' in the legs of Amblypygi; the presence of CZY in Mesothelae and Opisthothelae is a synapomorphy for them alone. The meaning of this is that *A. fimbriunguis* represents a clade of spiders forming the sister group to Mesothelae + Opisthothelae, and could justifiably be made the single member of a new suborder.

There are several interesting autapomorphies for the Devonian spider. Most obvious are the fimbriate claws, described above. These do not occur on any other spider known to us and differ strongly from the smooth claws of trigonotarbids. Secondly, the patches of acute spinules at the inner base of the palpal femora would appear to be unique among spiders. Somewhat worrisome, but a potential third autapomorphy, is the absence of trichobothria. It may be that they are present and we have not found them, but given our close examination of the material, this is extremely unlikely.

These additional observations have an effect on the cladogram published by Shear *et al.* (1987). One result has been to affirm the basal position in the cladogram of Trigonotarbida as the plesiomorphic sister group of all the other included orders of Pulmonata. The evidence lies in the lack of tarsal organs and lyriforms in trigonotarbids, and the presence of these features can be considered synapomorphic for the other orders. (However, if the 'tarsal organ' of scorpions and the

Haller's Organ in ticks are homologous to the tarsal organ of spiders, amblypygids and uropygids, then the loss of it may be an autapomorphy of trigonotarbids.) The basal, plesiomorphic position of the trigonotarbids, which in general resemble 'spiders without spinnerets', emphasizes the strongly derived nature of Amblypygi, Uropygi, and Schizomida.

Secondly, the earlier conclusion that the Amblypygi are the sister group of Uropygi + Schizomida, and not of Araneae, is reinforced. It can be further suggested that the key adaptations of the ancestor of the 'pedipalp' clade were the development of raptorial palps, probably articulating in the horizontal plane, antenniform first legs used as a ranging device for palpal strikes, and finally, as Manton (1977) wrote, partial or total immobilization of the patella–tibia joint to strengthen the knee, which must undergo extreme flexure in connection with the other modifications of legs to allow the animals to slip sideways into narrow crevices. In uropygids, the joints are far more mobile on legs 2–4 than in amblypygids, but the patella–tibia joint has been entirely lost in the first legs. Schizomids may be seen as a derived clade of uropygids; the movement of their palps in the vertical plane and the subdivision of the carapace are secondary changes designed to increase the flexibility of the whole body to allow for movement in the small spaces between soil particles. But the fused patellotibia of the first leg remains as a vestige of their common ancestry with uropygids.

It should also be recognized that naked cheliceral fangs, cheliceral glands, transversely oriented metatarsal lyriforms, and the presence of lyriforms on podomeres other than metatarsi, are probable autapomorphies of Araneae, joining the better known features of cheliceral poison glands, opisthosomal silk glands and spinnerets, and the palpal intromittent organ in mature males.

SYSTEMATIC PALAEONTOLOGY

Order ARANEAE Clerck, 1757

Emended diagnosis. Pulmonata with paired abdominal appendages modified as silk-spinning organs; chelicera with cheliceral gland; cheliceral fang with poison gland opening, and without setae; adult male palps modified for sperm transfer; numerous longitudinally oriented lyriform organs present on walking legs in addition to transverse one on distal metatarsus.

Genus ATTERCOPUS gen. nov.

Derivation of name. English dialect (from Old English) *attercop*, a spider.

Type and only known species. Attercopus fimbriunguis (Shear, Selden and Rolfe, 1987).

Diagnosis. Spider with patch of minute cuticular spinules on proximal infero-?anterior surface of palpal femur; minute cuticular fimbriae on inferior surface of all tarsal claws; without longitudinal emargination on posterior side of distal edge of patella of walking legs.

Attercopus fimbriunguis (Shear, Selden and Rolfe, 1987)

Plate 1; Plate 2, figs 1, 2, 4–8; Plate 3; Plate 4; Plate 5, figs 1–3, 5; Plate 6, figs 1, 2, 4, 5; Text-figs 4; 5A, B, D–H; 6; 7; 8; 9A, C; 10; 12.

1987 *Gelasinotarbus? fimbriunguis*, Shear, Selden and Rolfe; Shear *et al.*, pp. 60–65, 71, figs 128–140.
1987 Arachnida Incertae sedis B, Shear, Selden and Rolfe; Shear *et al.*, pp. 70, 71, figs 151–157.

Type specimens. Listed in Shear *et al.* (1987), p. 60.

Additional material. A complete list of the specimens referred to this species is deposited in the British Library, Boston Spa, Yorkshire, England, as Supplementary Publication No. SUP 14040, 5 pp.; see *Repository* above for availability of this publication.

Diagnosis. As for the genus.

Description

Cuticle. The cuticle pattern of *Attercopus fimbriunguis* is characteristic, and readily identifiable. The surface sculpture was described in Shear *et al.* (1987, p. 64) as being reticulate, with one side (distal, normally) of each polygonal cell being thicker than the other sides; the sculpture of Incertae sedis B was described (Shear *et al.* 1987, p. 70) as being similar. This sculpture pattern can be confirmed here, but with added detail: first, the distal side of each polygon of the reticulum actually forms the proximal side of the distally adjacent cells, and second, the sculpture dissolves into smooth cuticle in places, such as over most of the distal parts of the tarsus and the chelicera. Two distinct sizes of setal socket and the presence of long, fine setae without bifid tips were mentioned by Shear *et al.* (1987); the cuticle of Incertae sedis B was described as lacking this bimodality of setal sockets. The present study confirms that two sizes of setal sockets may be present, for example, on most of the leg segments there are small sockets with long, fine setae, and larger sockets bearing larger, long setae. This bimodality can, in fact, be seen on the published figures of Incertae sedis B (Shear *et al.* 1987, figs 151–154), but it is somewhat variable, and is not, alone, diagnostic for the genus. Many of the setae can be seen to be finely serrate, and the macrosetae bear serrae on their convex surface.

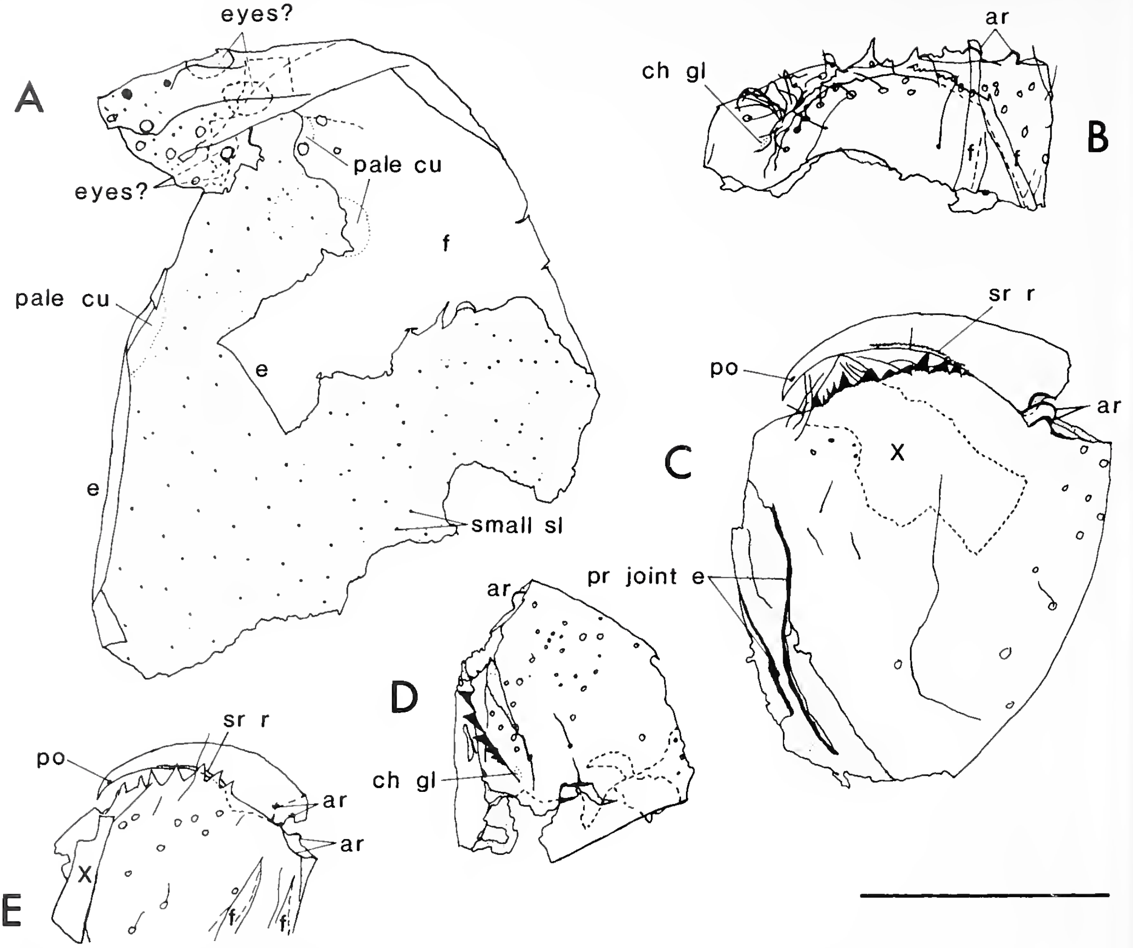
Most characteristic of *Attercopus fimbriunguis* is the presence of very small cuticular organs scattered across the cuticle surface (Pl. 1, fig. 1). Their distribution may be quite dense, for example on the spinneret (Text-figs 10 and 11A, B). At low magnification (up to about × 100), these appear very much like small setal sockets: a circle or oval of dark cuticle, about 0·006 mm in diameter. At higher magnification, however, the central pore is revealed as a slit, and thus these organs are true slit sense organs. In addition, larger slit sensilla are found at the joints. They may occur singly, at the distal end of the tarsus for example, in groups, such as those adjacent to the distal articulations of the femur, or in lyriform organs, examples of which can be seen at the distal ends of the patella, the tibia and the metatarsus. The distribution of the larger slits and lyriforms on the generalized leg is shown in the reconstruction (Text-fig. 2).

A major surprise in the present study was to find no evidence of trichobothria on any of the leg segments. The report of one on specimen 411.7.19 (Shear *et al.* 1987, p. 70) is incorrect; study of many more specimens of femora has shown that these podomeres are susceptible to the occurrence of circular dark patches, the origin of which is unknown, but which may be pre- or post-mortem fungal or parasitic attacks. That the dark patches occur only rarely, and then in different places on the same podomere (e.g. on palpal femora), is evidence that they are not a feature of *A. fimbriunguis*.

Carapace and abdomen. Three pieces of cuticle may represent parts of the carapace. 2002.12.102 is a sheet of typical reticulate *A. fimbriunguis* cuticle, with small slit organs scattered over the surface, which lacks setal sockets except at one end where large sockets occur, adjacent to two large, oval holes; nearby are what appear to be the edges of two further holes (Pl. 1, fig. 1). On one side of the specimen is an edge with a narrow doublure, and that part of the specimen which is folded over also has an edge to it. The holes are interpreted as possible eyes, and the edges as the carapace margin. The margin is not scalloped, as it is in trigonotarbids. A similar edge, with a narrow doublure, occurs on specimen 329.31. It is noteworthy that the carapace of *Liphistius* is almost devoid of setae except around the margins, and adjacent to the group of eyes (which are situated in the midline at the anterior edge of the carapace) some large setae are present. Specimen 411.11.3 is a chelicera of *A. fimbriunguis* which is superimposed on a large sheet of *A. fimbriunguis* cuticle. The cuticle sheet is torn down the centre and displaced so that it is overlapping; short lengths of edge can be seen on the sheet, but no eyes are present. Three characteristics suggest that this specimen belongs to the carapace: first, the size of the sheet in comparison to the size of the chelicera, second, the lack of podomere structures, and third, the features of the presumed carapace fragment 2002.12.102 mentioned above (lack of setal sockets except near the presumed anterior edge) also occur in this specimen.

Sternum. The sternum, which consisted of a cushion-like surface in life, occurs in the fossil as a rectangular strip of cuticle, about five times as long as wide (not all of it may be preserved), on specimen 411.19.83 (Pl. 2, fig. 2). Articulations are present at the points where the coxae meet the sternum. There are three pairs of these visible in the specimen, one side of each pair adjacent to each of the two coxae preserved. The anterior end does not preserve this feature, and the posterior end is missing. If the well-preserved coxa on this specimen belongs to leg 4 (see below), then the sternum is probably produced backward between coxae 4.

Chelicera. The chelicera (Pl. 1, figs 2–8) is equant in shape. Specimen 334.1*a*.7 is nearly complete and shows proximal articulations along a joint plane which is nearly at right-angles to the tooth row. The articulations



TEXT-FIG. 4. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated on Plate 1. A, 2002.12.102, anterior part of carapace, small slit sensilla shown on internal surface only. B, 2002.12.90, distal end of chelicera. C, 445.1*a*.7, whole chelicera with fang, proximal joint edges shown at left (near side is partly detached), foreign cuticle fragment (X) lying behind specimen. D, 411.7.33, nearly complete chelicera lacking fang, showing tooth row and cheliceral gland (both on far side). E, distal end of chelicera with fang, tooth row (distal end partly obscured by artefact). Scale bar represents 0.5 mm for all specimens; see MATERIALS AND METHODS for abbreviations and conventions.

EXPLANATION OF PLATE 1

Figs 1–8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, anterior part of carapace showing possible eyes and large setal sockets at anterior, also typical cuticle sculpture and small slit sensilla elsewhere, explanatory drawing in Text-figure 4A, 2002.12.102, × 70. 2, distal end of chelicera showing tooth row, fang articulations, and position of cheliceral gland, explanatory drawing in Text-figure 4B, 2002.12.90, × 107. 3, distal end of tooth row of specimen shown in fig. 2, showing cheliceral gland, 2002.12.90, × 215. 4, chelicera, lacking fang, showing general shape, tooth row, and position of cheliceral gland, explanatory drawing in Text-figure 4D, 411.7.33, × 95. 5, distal end of tooth row of specimen shown in fig. 3, showing cheliceral gland at end of tooth row, 411.7.33, × 235. 6, whole chelicera, showing general shape, articulation of fang, and poison gland opening, foreign cuticle fragment lying across part of tooth row, explanatory drawing in Text-figure 4C, 334.1*a*.7 × 55. 7, distal part of chelicera showing tooth row, fang articulation, poison duct opening, and serrated ridge on fang, artefact lying across distal end of tooth row, explanatory drawing in Text-figure 4E, 329.22.9, × 132. 8, distal part of specimen shown in figure 6, showing details of fang articulation, poison gland opening, serrate ridge, and tooth row, 334.1*a*.7 × 105.

PLATE 1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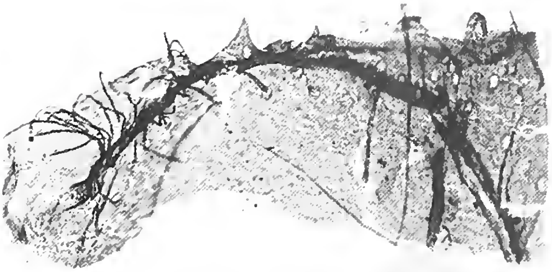
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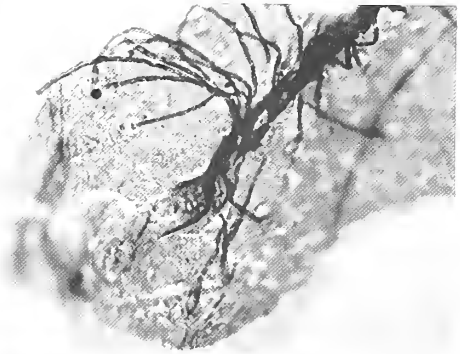
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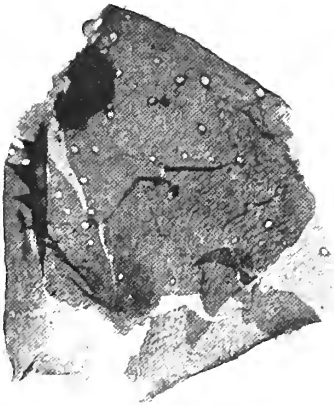
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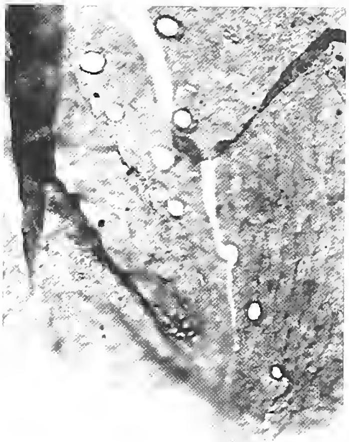
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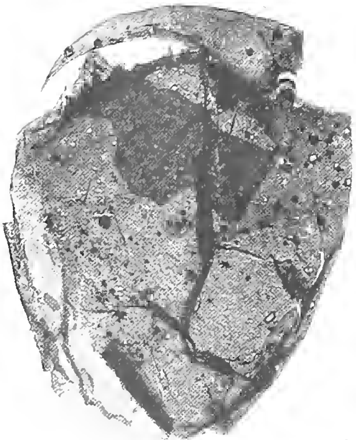
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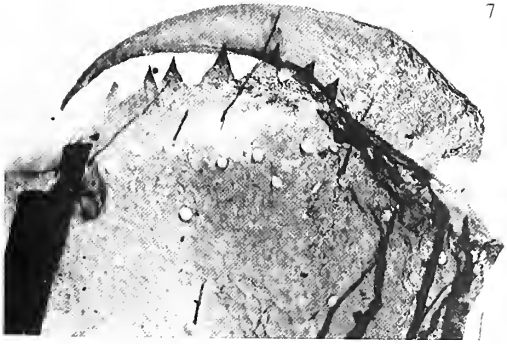
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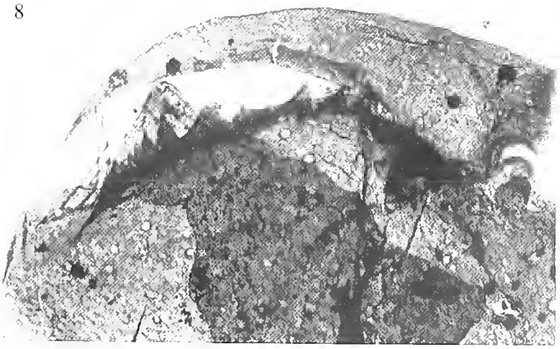
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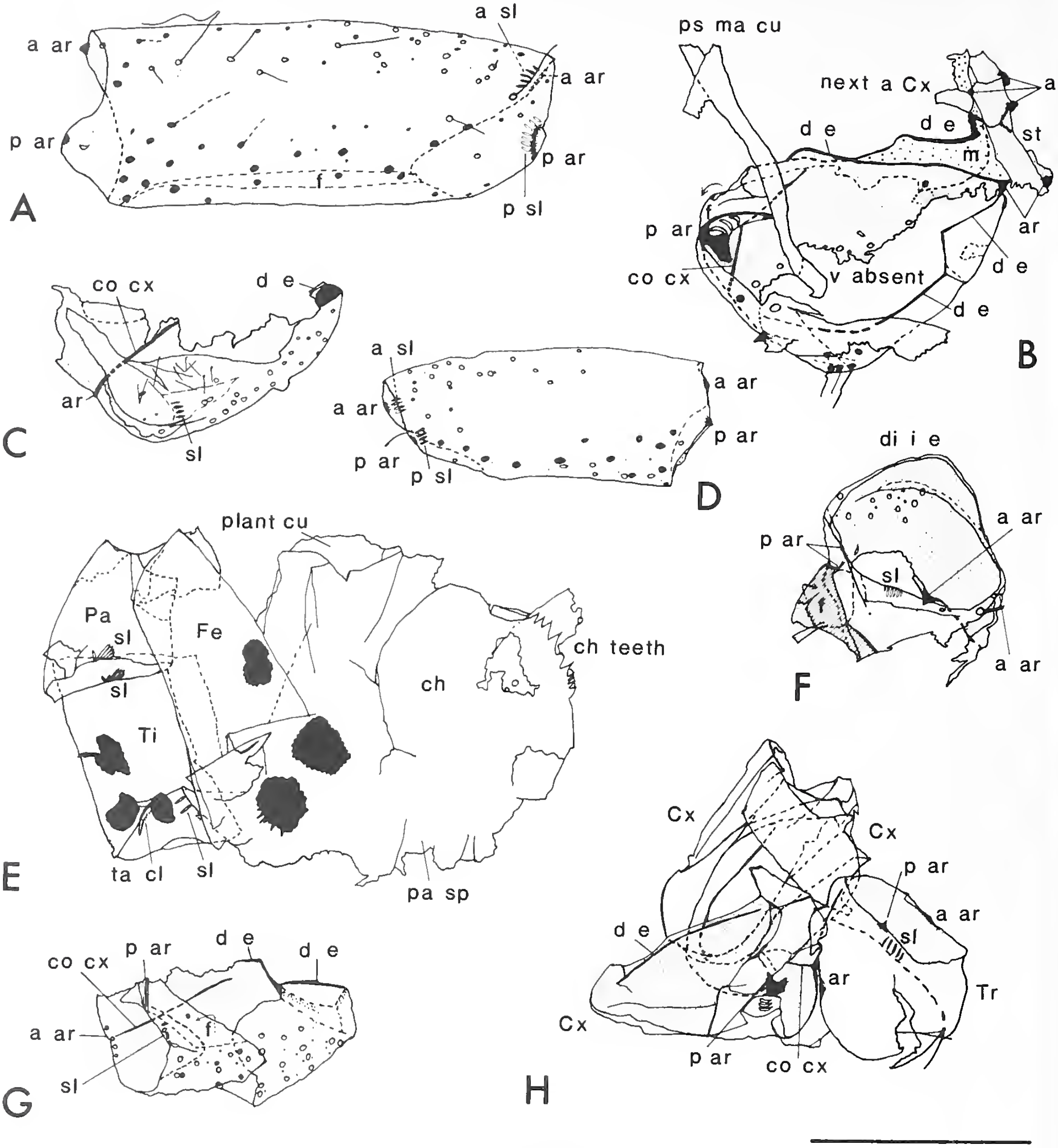
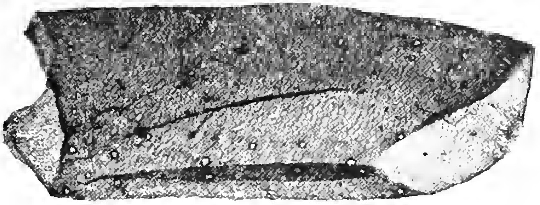


TEXT-FIG 5. For legend see p. 262.

EXPLANATION OF PLATE 2

Figs 1, 2, 4–8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, femur in posterior aspect, distal to right, explanatory drawing in Text-figure 5A, 334.1*a*.9, ×64. 2, left coxa (probably of leg 4), sternum (top to right), fragment of coxa ?3, and piece of marginal cuticle of prosoma, posterior aspect, explanatory drawing in Text-figure 5B, 411.19.83, ×62. 4, femur, posterior aspect, distal to left, explanatory drawing in Text-figure 5D, 334.1*a*.6, ×93. 5, complex grouping of podomeres, including chelicera (dark mass on right), palpal femur, leg ?2 femur, patella, tibia, and tarsus (all on left), and plant cuticle and spores, explanatory drawing on Text-figure 5E, 329.69, ×80. 6, trochanter, distal aspect, inferior to top, fragment of coxa attached at bottom left, explanatory drawing in Text-figure 5F, 411.19.102, ×93. 7, three coxae (two at top, one at bottom left) and trochanter (bottom right), explanatory drawing in Text-figure 5H, 334.1*a*.9, ×66. 8, coxa, posterior aspect, explanatory drawing in Text-figure 5G, 411.19.250, ×117.

Fig. 3. *Ecchosis pulchribothrium* gen. et. sp. nov. Ventral part of coxa, posterior aspect, explanatory drawing in Text-figure 5C, 2002.9.13, ×110.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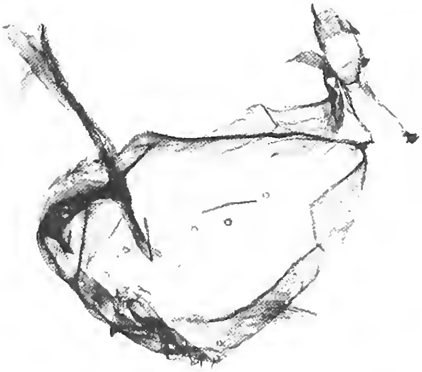
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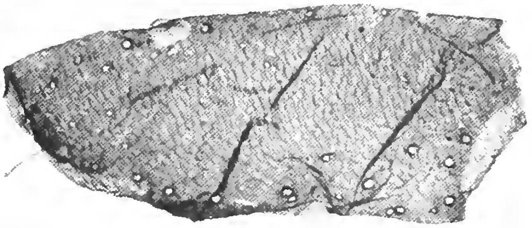
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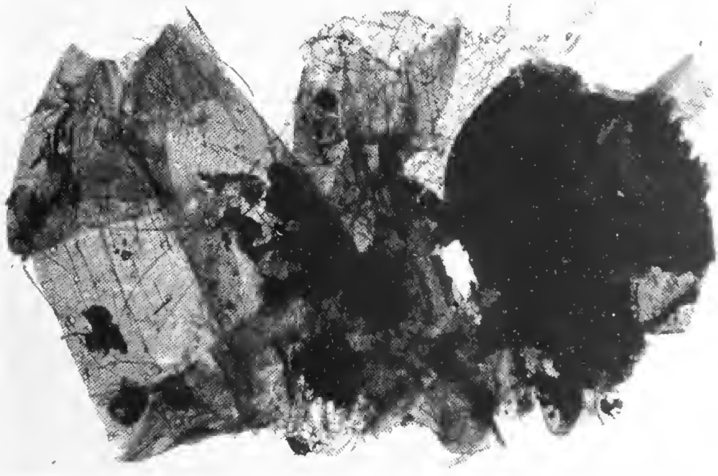
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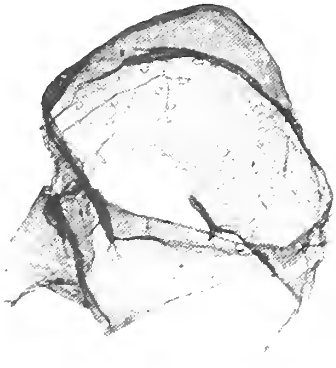
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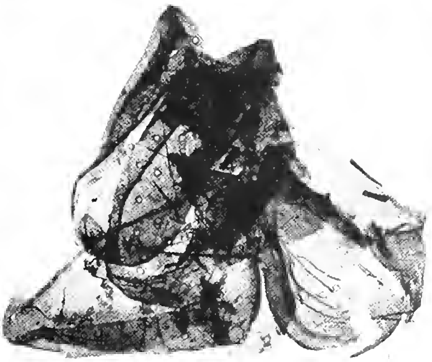
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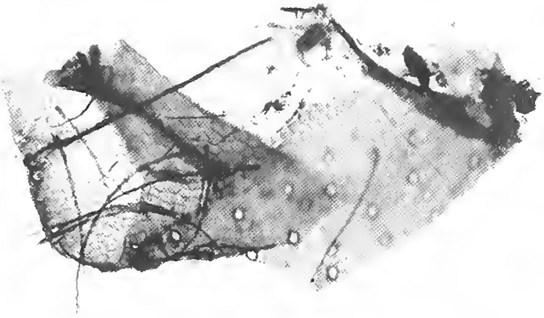
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SELDEN *et al.*, *Attercopus*, *Ecchosis* are arranged in such a way that it is difficult to envisage this chelicera being anything other than orthognath. The teeth are in a single row of about 8–11 teeth (8 in small, 11 in large specimens). The smallest teeth occur near the fang tip, the larger occur closer to the basal articulation of the fang, and largest of all is third or fourth from the end of the row nearest the fang articulation. There are no subsidiary teeth, and the teeth are not greatly different in size, the smallest is about half the size of the largest. The fang curves gently to a point adjacent to end of tooth row. A possible orifice for the poison gland may be seen subterminal to the fang tip on specimens 334.1*a*.7 and 329.22.9 (Pl. 1, figs 7 and 8); other specimens do not show the fang tip. The inner surface of the fang bears a ridge of fine serrations extending the length of the tooth row. Most of the cuticle surface bears only a sparse scattering of setal sockets; setae are numerous near the teeth, but do not occur in a comb or brush. The setae are finely serrate. There are no setae on the fang. The cheliceral gland openings can be seen on specimens 2002.12.90, 329.31*a*.M1, and 411.7.33 at the end of the tooth row near the fang tip (Pl. 1, figs 3 and 5). A few slit sensilla occur adjacent to the fang articulations.

Coxa. Coxae are present on a number of specimens, but commonly these bear numerous other podomeres compressed together (on Pl. 2, fig. 7 three coxae and a trochanter occur together), so the coxal morphology is better interpreted from the few isolated examples (e.g. Pl. 2, figs 2 and 8). Understanding the coxal morphology is aided by study of the coxa of *Liphistius* in conjunction with the fossils. The coxa on specimen 411.19.83 probably belongs to leg 4, since it occurs at the rear of the sternum (see below) which appears to have attachment points for at least two, and probably three, coxae in front. If this coxa is not leg 4 then it would be leg 3. Adjacent, and anterior to, the main example on this specimen, is a small portion of the medial side of the next coxa anterior, also attached to the sternum, with some membrane between the two. The coxa is of the boat-like form typical of most arachnids, although on this specimen the ventral surface is mainly missing. The anterior dorsal edge runs with a thickened line from an attachment point with the sternum towards the distal margin, but about two-thirds of the way along towards the distal margin, it dips ventrally; the next part up to the distal edge is missing. The posterior dorsal edge is also thickened in a line, which runs horizontally for about one-third of the way to the distal edge then dips towards the ventral, for a distance of about half the length from the sternum to the dip, and then runs to the distal edge at this lower elevation. Specimen 411.19.250 (Pl. 2, fig. 8) is most useful for reconstructing the shape of the podomere. The anterior articulation at the distal joint lies at the end of a long ridge of thickened cuticle (the costa coxalis) which extends in a proximodorsal direction towards, and closely approaching, the anterior dorsal edge. The posterior articulation consists of a sclerite which originates at the posterior edge of the joint in an anterior position, and runs dorsally, separated from the joint edge by membrane (see Pl. 2, fig. 8). The morphology of the distal joint is very similar to that of the Recent *Liphistius*. The strip of cuticle running along the dorsal side of the coxae, the lateral marginal plate, and also seen in *Liphistius*, can be seen on 411.19.83. On this specimen the posterior sclerite is folded onto the anterior side of the distal joint.

Trochanter. Trochanter morphology is difficult to interpret because so many of the few specimens are folded together with coxae or femora. The best specimens are 334.1*a*.9 (Pl. 2, fig. 7), which is attached to coxae, but relatively easy to make out, and 411.19.102 (Pl. 2, fig. 6), a separate trochanter. The trochanter is a short podomere, the inferior surface is nearly twice as long as the superior and was bulbous in life. The interior surface bears numerous large setal sockets. Proximal articulations consist of a prominent, thick triangular projection which marks the anterior articulation, slightly inferior in position; the posterior articulation shows

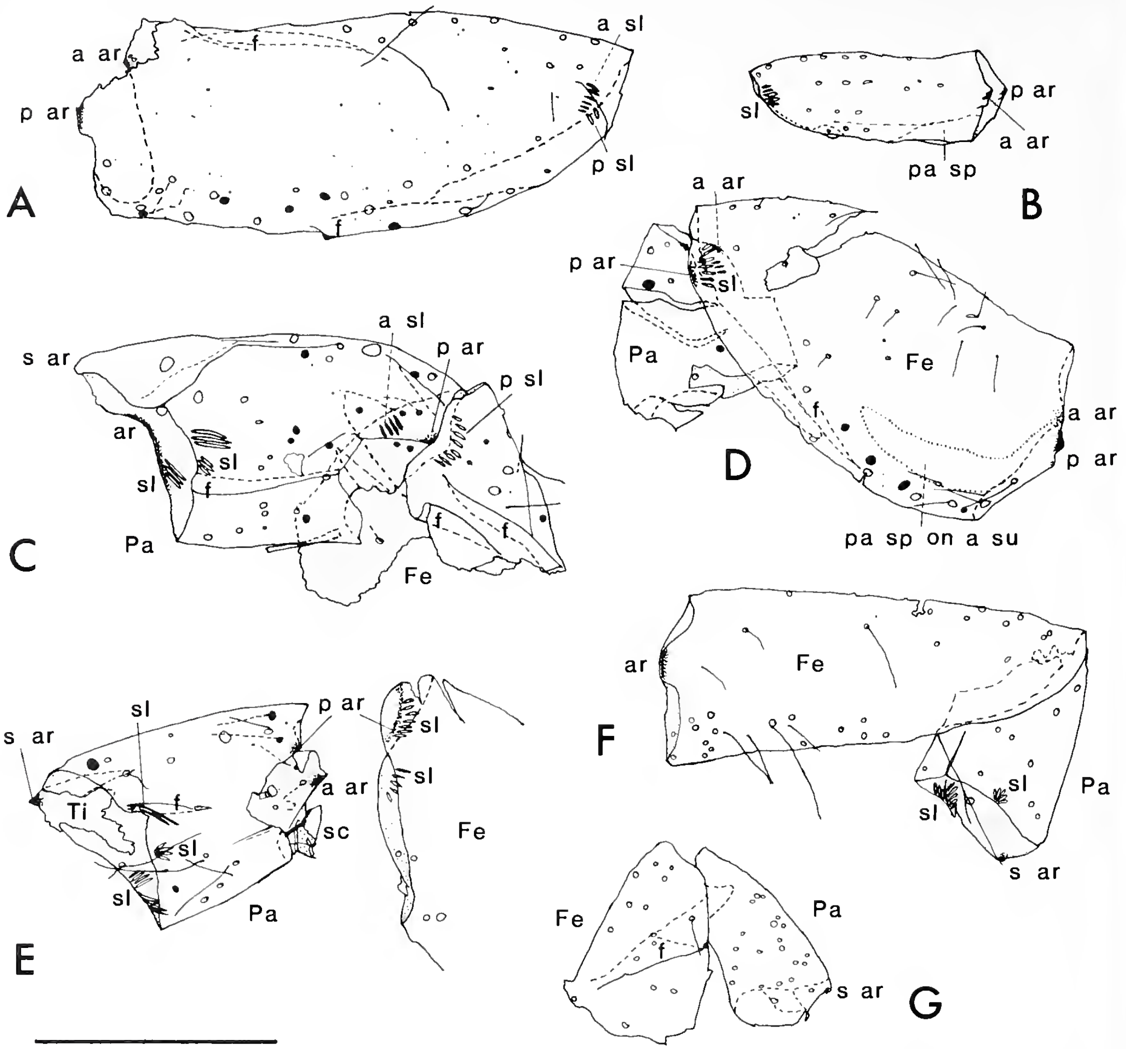
TEXT-FIG. 5. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (A, B, D–H) and *Ecchosis pulchribothrium* gen. et sp. nov. (C), explanatory drawings for specimens illustrated on Plate 2. A, 334.1*a*.9, femur of walking leg, posterior aspect. B, 411.19.83, left coxa (of leg 4?), sternum, fragment of next anterior coxa, and piece of marginal prosomal cuticle (folded and twisted), ventral surface of coxa ?4 absent. C, 2002.9.13, ventral part of coxa of *Ecchosis*, ventral surface to lower right, distal joint to left (superior side absent), spore in black. D, 334.1*a*.6, femur of walking leg, posterior aspect. E, 329.69, complex group of podomeres (setae omitted), plant cuticle, spores (in black). F, 411.19.102, trochanter, distal aspect, inferior to top, posterior to left, including fragment of coxa (shaded) with posterior articulation. G, 411.19.250, ventral half of coxa, torn and folded, posterior aspect, inferior to lower right, distal joint to left (superior side absent), setae omitted. H, 334.1*a*.9, three coxae and trochanter, two coxae at top, one at lower left, trochanter at lower right, setae and interior surfaces of upper two coxae omitted. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

only as a darkened edge, the major part of this being on the coxal side of the joint. However, 411.19.102 (Pl. 2, fig. 6) shows a portion of the coxa attached at this point, and reveals the detail of the articulation well. The distal joint bears anterior and posterior articulations; these are not well expressed, being only dark but discrete edges to the podomere. They are connected by a fold of cuticle on the inferior edge which marks the distal termination of the bulbous part of the inferior surface. Superoanteriorly on the distal edge there is a group of slit sensilla; a group of slit sensilla occurs in exactly the same position in *Liphistius*, and is useful for identifying the orientation of loose podomeres. Specimen 329.59, which was figured by Shear *et al.* (1987, fig. 140) as a possible median organ of some kind, is now reinterpreted as half of a trochanter. The cuculliform shape described by Shear *et al.* (1987, p. 64), is incorrect, since there is only a single layer of cuticle present, the inferior surface of the trochanter, and basally, the two proximal articulations can be seen.

Femur. The femur is an easily recognizable podomere, and occurs on many slides. The characteristic palpal femur, with a patch of spinules, is described below. The femur is a long podomere, with a bicondylar horizontal pivot joint proximally (Pl. 3, fig. 8) and a greatly inferiorly emarginated distal joint with a dorsal bicondylar hinge. Specimens 334.1*a*.6, 334.1*a*.9, 2002.12.79, and 329.3 (Pl. 2, figs 1 and 4; Pl. 3, figs 1 and 2) show typical podomeres. Longitudinal rows of setal sockets occur on the superior surface, and similar rows are found on the inferior surface. The anterior and posterior sides are devoid of setae. The articulations on the proximal joint occur on pronounced promontories. The distal joint bears curved rows of slit sensilla adjacent to the articulations, which are situated superoposteriorly and superoanteriorly. Fewer slits occur in the anterior group than in the posterior. Some variation in the femora is noticeable, in greater or lesser amounts of emargination at the inferior side of the distal joint. This can be accounted for by differences between the legs. In *Liphistius*, the emargination is greatest on legs 2 and 3, whereas on leg 4 and on the palp there is less emargination; the least emargination of all occurs on leg 1. The amount of emargination is correlated with the degree of flexure required during stepping of the legs, and the activities of the palp. Specimen 329.31*a*.M1 (Pl. 3, fig. 7) shows a femur with little emargination in connection with a chelicera and palpal femora; this presumably belongs to leg 1.

The palpal femur is not very large (the largest is specimen 329.63, figured in Shear *et al.* 1987, fig. 155), and bears a patch of cuticular spinules on its proximal infero-?anterior surface (Pl. 3, fig. 4). The spinules are not setae, but cuticular projections, and were figured by Shear *et al.* (1987, figs 156 and 157). By assuming that these were used towards the mouth or towards the anterior/mesal, then they would be on the inner, proximal prolateral side. The bases for the supposition that this podomere is palpal are, first, that modifications to the prosomal limbs in spiders are more likely to affect the palp than any other leg, and second, that when this podomere is found connected together with other organs, it is found adjacent to the chelicera in all cases. Apart from the patch of spinules, the palpal femur is similar to the other femora. There is a bicondylar pivot joint with a horizontal axis at the proximal end of the podomere, and a superior bicondylar hinge distally, with a greatly emarginated inferior surface. Rows of slit sensilla occur adjacent to the distal articulations. Setae on the podomere occur in rows; principally two rows superiorly, two inferiorly, and one retrolaterally. Specimens 329.3 (Pl. 3, fig. 2) and 329.63 show right femora, and 329.1 (Pl. 3, fig. 4) shows the left femur in connection with the patella. Two palpal femora are present on 329.31*a*.M1, together with the chelicera, and other podomeres.

Patella. The patella is a short podomere, with the curved superior surface more than twice the length of the inferior surface. Specimens are shown on Plate 3, figures 3–7, and Plate 4, figures 2 and 5. The proximal joint bears superoanterior and superoposterior articulations corresponding to those distally on the femur. The inferior part of this joint, however, is emarginated, more so posteriorly than anteriorly, and two dark, recurved areas are present in inferoposterior and inferoanterior positions. By comparison with living spiders, amblypygids, and uropygids, these areas mark the sites of suspension of the arcuate sclerite: a distally procurved sclerite lying in the membrane of the greatly emarginated Fe–Pa joint, and facilitating flexion from the extreme extension possible at this joint. The sclerite itself seems unlikely to be preserved, but nevertheless, one appears to be present on specimen 329.31*a*.M1, on leg ?1 (Pl. 3, fig. 7). Distally, there is a strong superior articulation; the distal joint is not a bicondylar pivot, as stated by Shear *et al.* (1987, p. 63), but is monocondylar. Three lyriform organs are situated in an inferoposterior position, and two occur inferoanteriorly, on the distal joint. Of especial interest here, is the lack of a pronounced emargination (CZY) on the posterior side of the distal joint, seen in *Liphistius* and all other spiders. In this respect, the *A. fimbriunguis* patella more closely resembles that of the ambulatory legs of uropygids. The superior surface bears about four large setae in addition to the smaller ones. Smaller setae occur elsewhere, especially superoproximally and inferiorly.

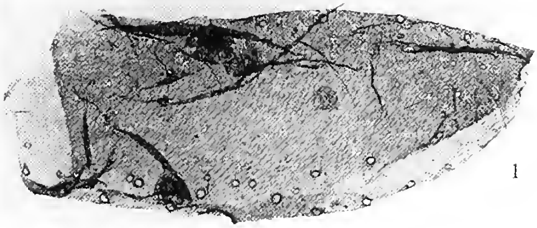


TEXT-FIG. 6. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated on Plate 3. A, 2002.12.79, posterior aspect of right walking leg femur, spores omitted. B, 329.3, anterior aspect of right palpal femur, spore omitted. C, 329.59, distal end of left femur and attached patella, posterior aspect. D, 329.1, posterior aspect of left palpal femur and attached patella, spores omitted. E, 329.31*a*.M1, detail of joints of left femur and patella, including, sclerite, posterior aspect. F, 334.1*b*.86, femur and patella, foreign cuticle omitted. G, 334.1*b*.12, distal femur and patella. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

EXPLANATION OF PLATE 3

Figs 1–8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, femur, posterior aspect, distal to right, circular spores attached, explanatory drawing in Text-figure 6A, 2002.12.79, ×84. 2, right palpal femur, anterior aspect, distal to right, patch of spinules on near (anterior) surface, black spore attached, explanatory drawing in Text-figure 6B, 329.3, ×133. 3, distal end of femur, patella, posterior aspect, explanatory drawing in Text-figure 6C, 329.59, ×73. 4, left palpal femur and patella, patch of spinules on far (anterior) surface, dark spores attached, explanatory drawing in Text-figure 6D, 329.1, ×74. 5, distal end of femur and patella, explanatory drawing in Text-figure 6G, 334.1*b*.12, ×115. 6, femur and patella, foreign cuticle fragment overlying proximal part of femur, explanatory drawing in Text-figure 6F, 334.1*b*.86, ×71. 7, part of complex grouping of podomeres showing distal femur and patella, posterior aspect, distal to left, details including sclerite at proximal joint of patella, distal patella with attached fragment of tibia, explanatory drawing in Text-figure 6E, 329.31*a*.M1, ×68. 8, proximal end of femur showing large setal sockets, 411.19.243, ×60.

PLATE 3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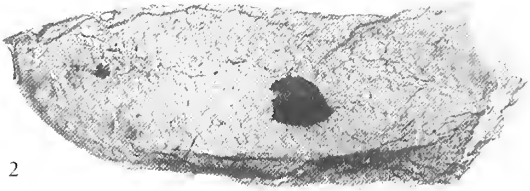
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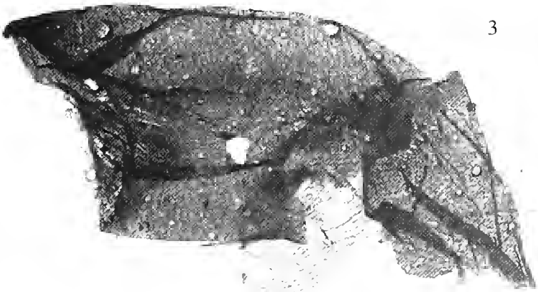
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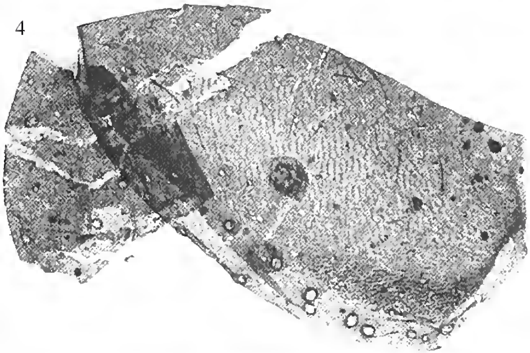
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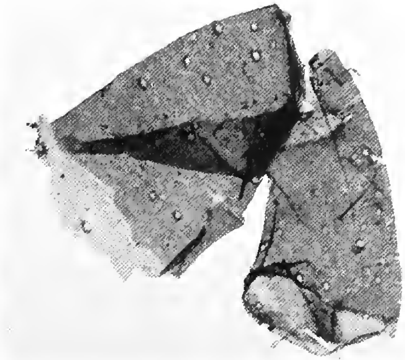
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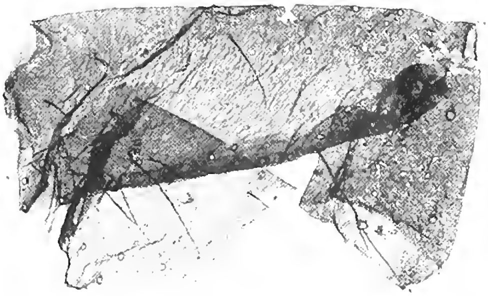
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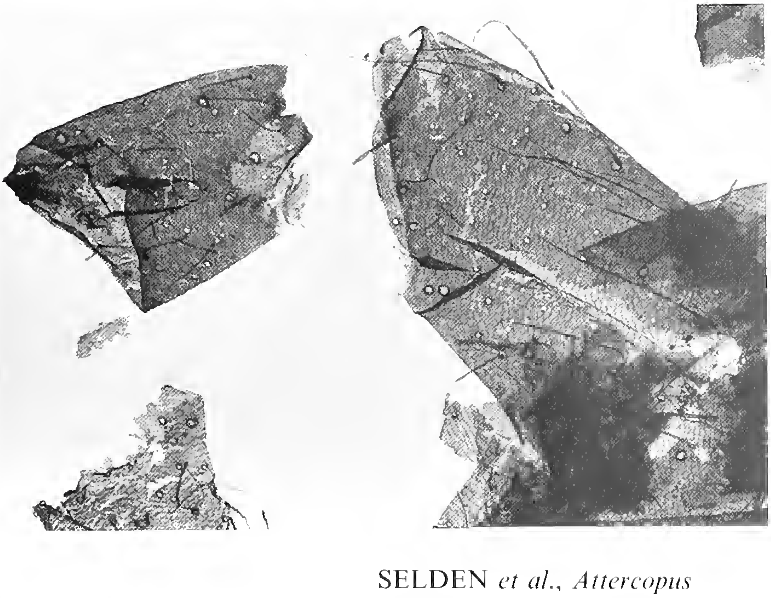
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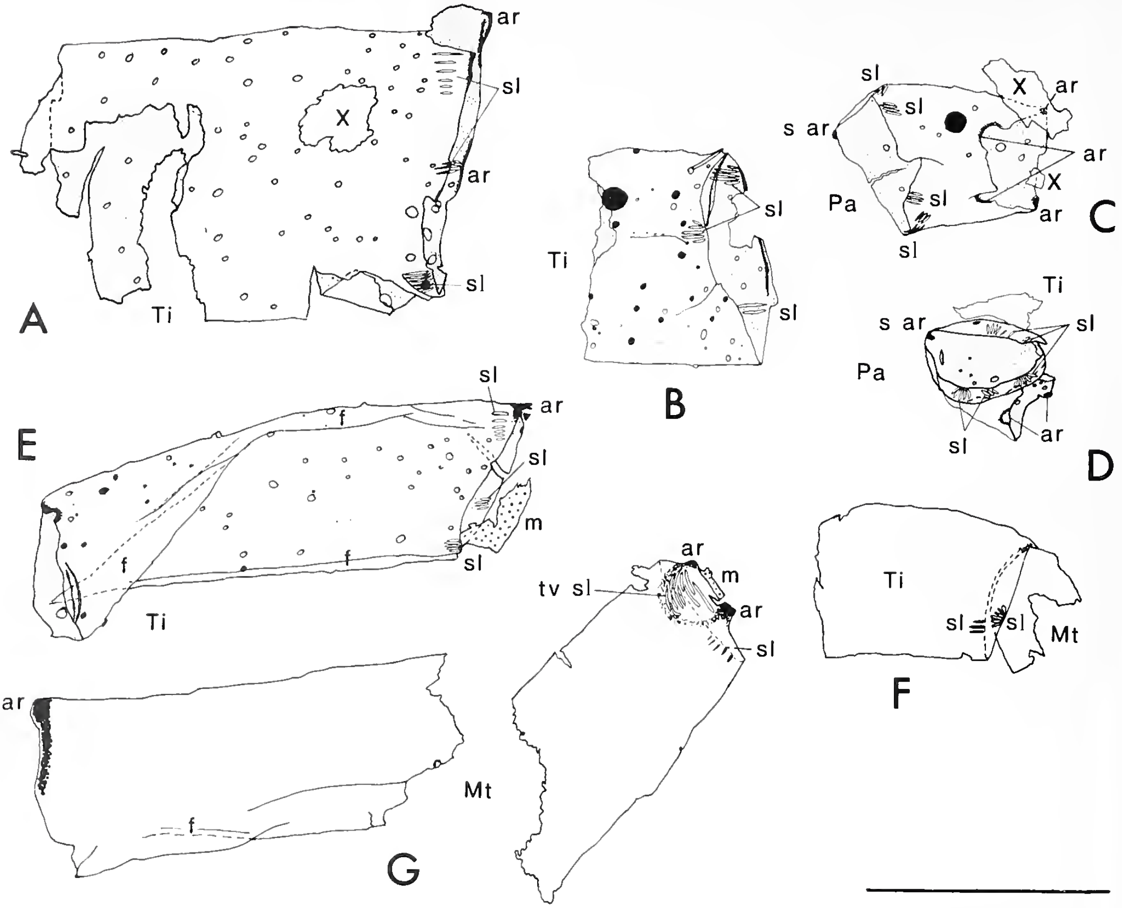
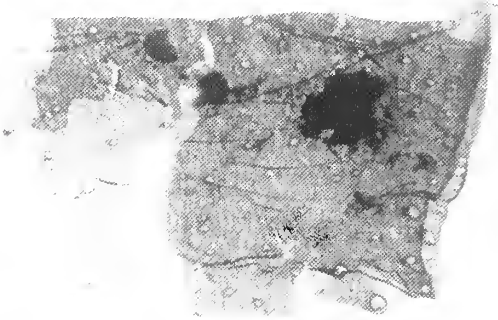
SELDEN *et al.*, *Attercopus*



TEXT-FIG. 7. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated on Plate 4. A, 329.3, distal end of tibia, detritus shown at X, setal sockets not differentiated according to surface and setae omitted. *B*, 411.7.45, distal end of tibia, inferior aspect, spore shown in black. C, 411.20.25, patella, inferior aspect, spore shown in black, detritus by X. D, 411.19.248, distal aspect of patella, focused to show details of distal joint, superior to left. E, 334.1*a*.8, tibia, setae omitted. F, 411.19.98, distal end of tibia and proximal piece of metatarsus, superior aspect, setae and sockets omitted. G, 329.3, metatarsus, proximal end to left, distal to right, superolateral aspect, setal sockets omitted. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

EXPLANATION OF PLATE 4

Figs 1–11. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, distal end of tibia, dark mass of detritus, explanatory drawing in Text-figure 7A, 329.3, ×70. 2, patella, inferior aspect, distal to left, pieces of detritus on right, and spore, explanatory drawing in Text-figure 7B, 411.20.25, ×132. 3, distal end of tibia, showing sensilla and articulations, spore in top left, explanatory drawing in Text-figure 7C, 411.7.45, ×125. 4, distal end of tibia showing sensilla, 2002.12.49, ×65. 5, patella, details of distal joint, explanatory drawing in Text-figure 7D, 411.19.248, ×190. 6, tibia, distal to right, explanatory drawing in Text-figure 7E, 334.1*a*.8, ×66. 7, distal end of tibia attached to proximal part of metatarsus, superior aspect, explanatory drawing in Text-figure 7G, 411.19.98, ×124. 8, metatarsus, distal to left, attached spore at top, 329.38, ×58. 9, metatarsus, distal to left, 329.53, ×53. 10, metarsus, broken into two parts, distal to right, superolateral aspect, explanatory drawing in Text-figure 7F, 329.3, ×46. 11, metatarsus, superolateral aspect, distal to left, 411.19.251, ×92.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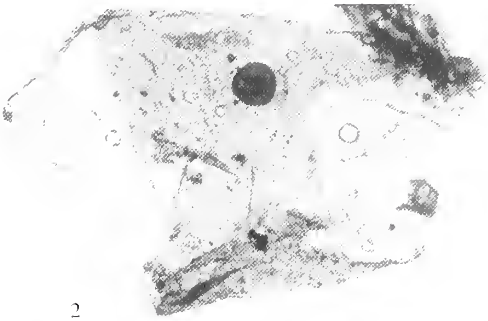
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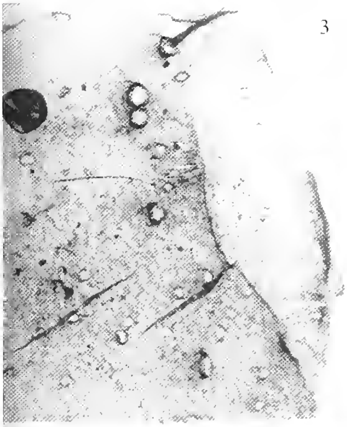
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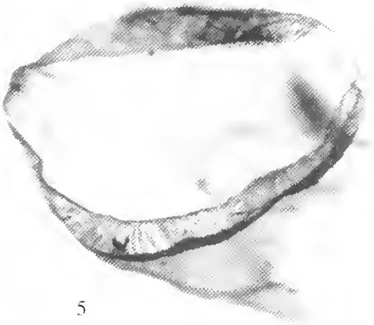
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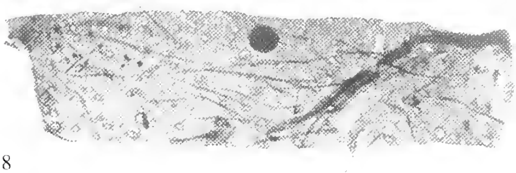
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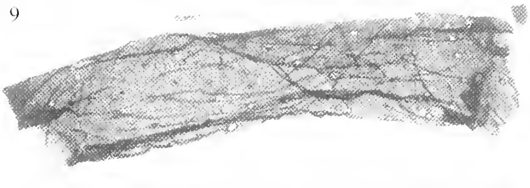
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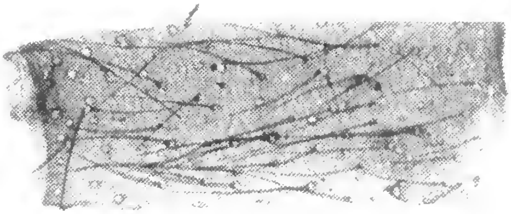
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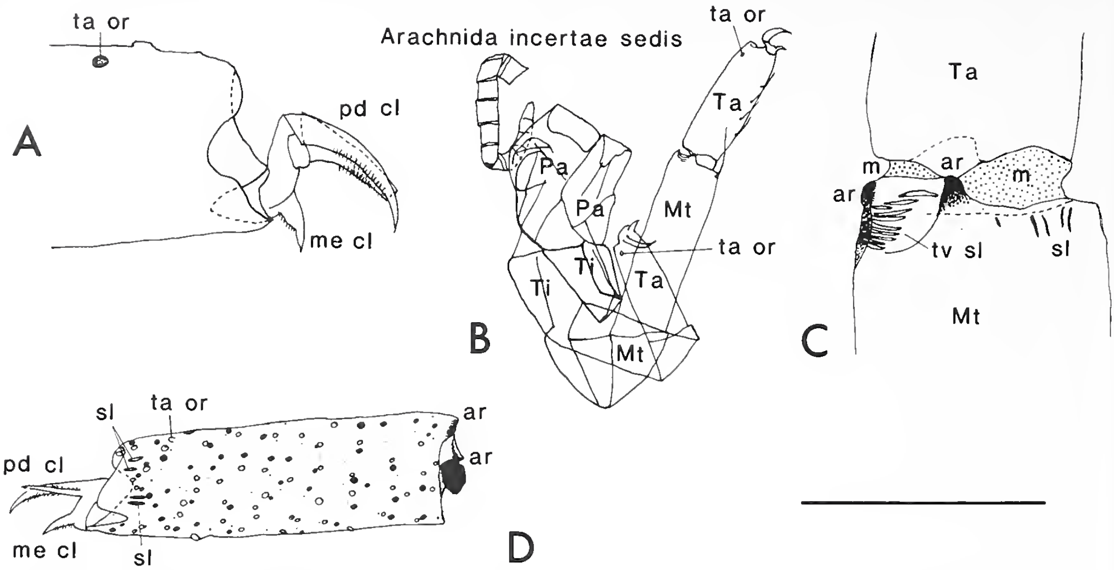
SELDEN *et al.*, *Attercopus*



TEXT-FIG. 8. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (A–D) and Arachnida *incertae sedis* (B), explanatory drawings for Plate 5. A–C, 334.1*a*.4, two walking legs, patella to tarsus; A, detail of distal end of tarsus, setae, sockets, and slit sensilla omitted; B, complete specimen with adjacent Arachnida *incertae sedis* flagelliform appendage, setae and sockets omitted for clarity; C, detail of metatarsus–tarsus joint, distal to top, setae and sockets omitted, arthrodial membrane shown in coarse stipple. D, 334.1*b*.38, tarsus, showing tarsal organ and slit sensilla, setae omitted, spore at proximal end. Scale bar represents 0.25 mm for A and C, 1.5 mm for B, and 0.5 mm for D; see MATERIAL AND METHODS for abbreviations and conventions.

Tibia. This podomere is about three times as long as wide (Pl. 4, fig. 6). When flattened in the fossils, it appears rectangular, lacking the distal emargination and the proximal promontories of the femur. It can be distinguished from the metatarsus by the superodistal lyriform organ of the latter, which has the slit sensilla arranged transversely. The proximal joint of the tibia bears a strong superior articulation. The distal joint is a superior bicondylar hinge. Adjacent to one side of the distal articulations is a row of slit sensilla, and there are lyriforms situated close to the inferior on this side, and on the opposite side of the joint in an anterior/posterior position. Features of the distal joint are shown on Plate 4, figs 1, 3, 4, 9. It is not possible to orient the tibia since the only specimens which are in direct connection with the patella and also preserve the distal joint are obscured by other podomeres.

Metatarsus. The metatarsus is the longest podomere on the leg, the longest being nearly four times as long as wide, in the flattened state. The proximal joint is a superior bicondylar hinge (see tibia, above). The distal joint

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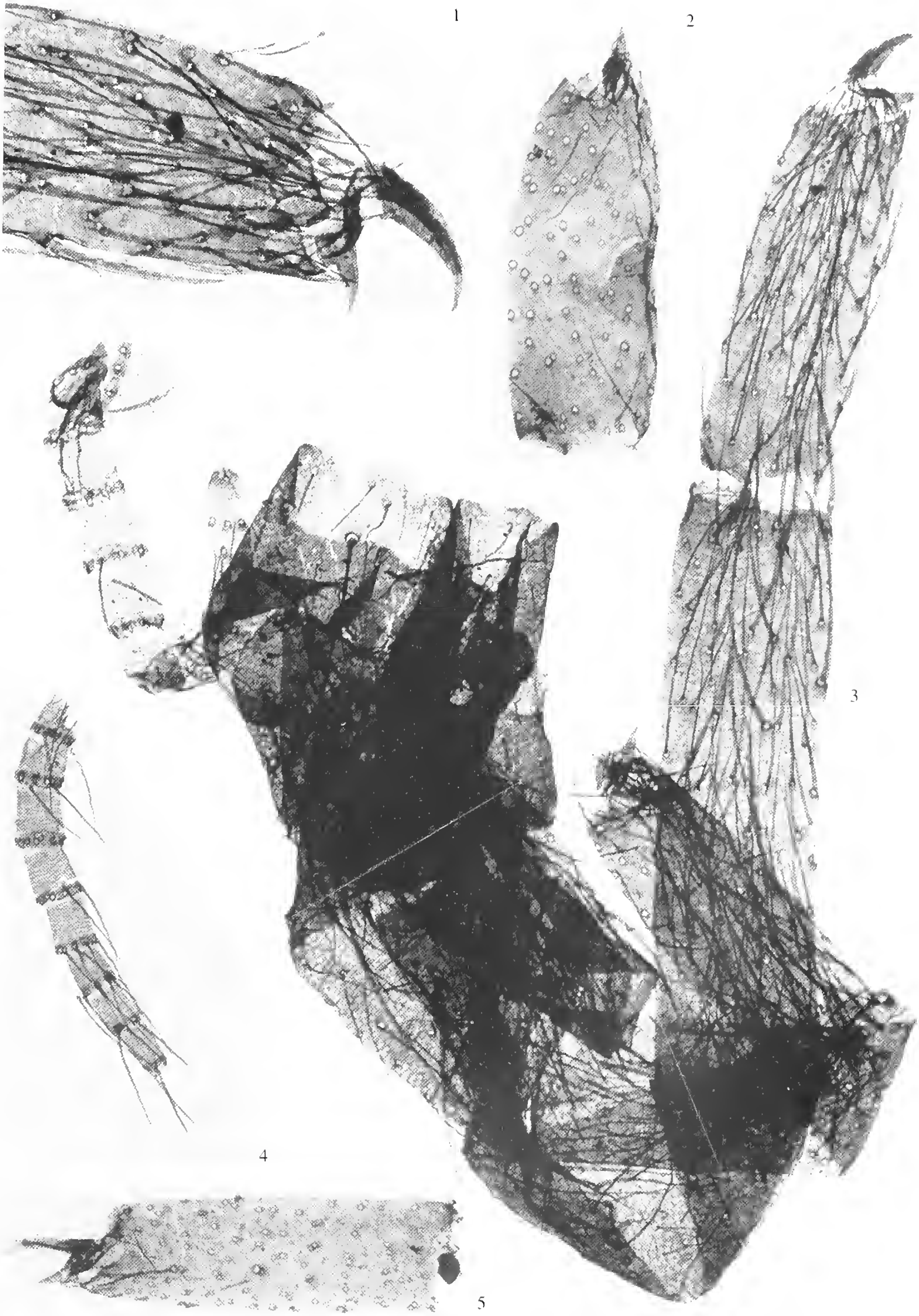
EXPLANATION OF PLATE 5

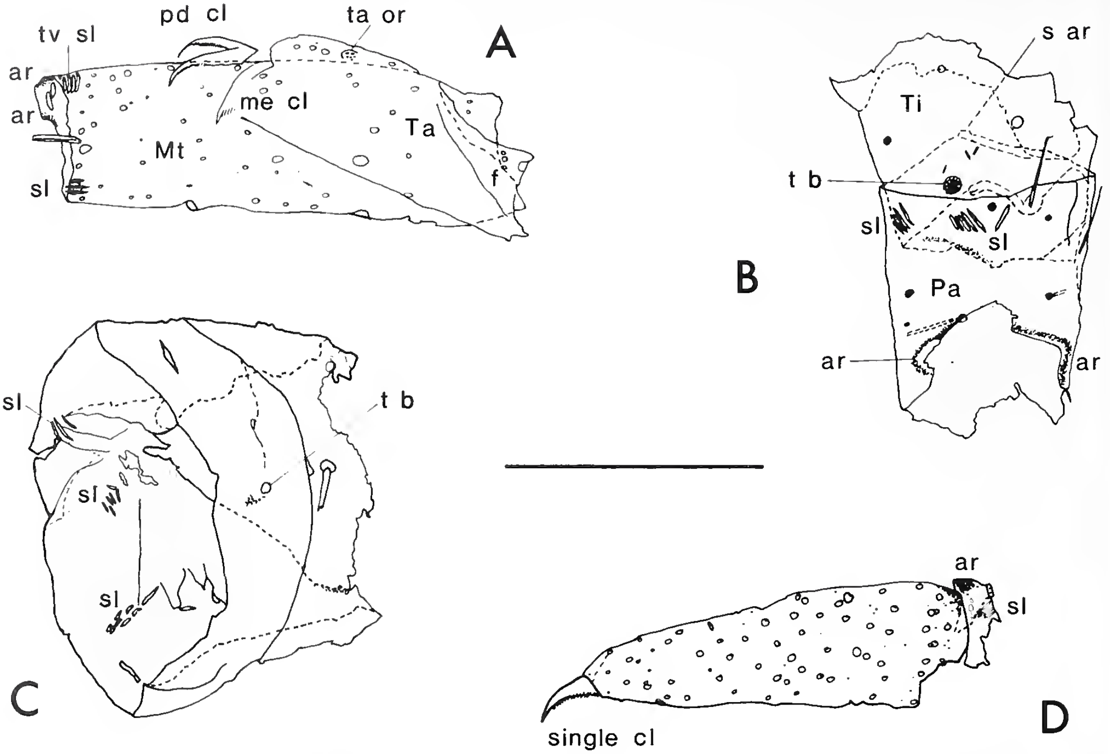
Figs 1–3, 5. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, detail of distal end of tarsus shown in upper part of fig. 3, showing setation, serrate macroseta inferiorly, tarsal organ superiorly, and arrangement of paired and median fimbriate claws, explanatory drawing in Text-figure 8A, 334.1*a*.4, ×165. 2, tarsus, distal to top, 329.16.34, ×92. 3, complex grouping of two walking legs of *Attercopus* with adjacent flagelliform appendate of Arachnida *incertae sedis*, explanatory drawing in Text-figure 8B, 334.1*a*.4, ×94. 5, tarsus, distal to left, showing tarsal organ, claws, spore at proximal end, explanatory drawing in Text-figure 8D, 334.1*b*.38, ×76.

Figs 3 and 4. Arachnida *incertae sedis*. 3 flagelliform appendage with 12 segments (including distal?), showing setae and slit sensilla, adjacent to legs of *Attercopus*, explanatory drawing in Text-figure 8B, 334.1*a*.4, ×94. 4, 8-segmented flagelliform appendage (including distal?), showing setae and slit sensilla, 2002.9.20, ×80.

PLATE 5



SELDEN *et al.*, *Attercopus*, Arachnida incertae sedis



TEXT-FIG. 9. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (A, D) and *Ecchosis pulchribothrium* gen. et. sp. nov. (B, C), explanatory drawings for Plate 6. A, 411.02.12M.6, metarsus and overlying tarsus, setal sockets not differentiated according to surface and setae ommited. B, 411.7.37, patella and proximal end of tibia, inferior aspect, distal to top. C, 411.19.96, patella, superior aspect, distal to left. D, 329.69, palpal tarsus, setal sockets not differentiated according to surface and setae omitted. Scale bar represents 0.5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

is readily recognized by the large lyriform organ situated in a superior position, which characteristically has the slits arranged at right angles to the long axis of the leg. The lyriform is situated at the base of a cuticular projection which bears articulations at either side (Pl. 4, figs 8–11; Pl. 5, fig. 3; Pl. 6, fig. 1). Though resembling a bicondylar hinge, the arrangement here is actually a rocking joint. As in spiders, the two 'condyles' are projections which articulate with the tarsus only loosely, the joint being held by muscles, and the joint allows rocking in an antero-posterior direction as well as flexure, as necessary (see Manton 1977; Clarke 1984, 1986). The metatarsus is well clothed with setae, some of which are long and thin, and macrosetae are present

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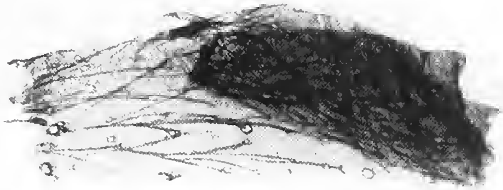
EXPLANATION OF PLATE 6

Figs 1, 2, 4, 5. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). 1, metatarsus and overlying tarsus, distal to left, explanatory drawing in Text-figure 9A, 411.02.12M.6, ×60. 2, detail of distal end of tarsus shown in fig. 1, showing claw fimbriae and tarsal organ, explanatory drawing in Text-figure 9A, 411.02.12M.6, ×154. 4, complex grouping of walking leg podomeres, including tibiae, metatarsi, and tarsi, showing setae, claws, and tarsal organs, 329.31*a*.M2, ×98. 5, palpal tarsus, showing attachment to metatarsus fragment, setae, and single fimbriate claw, explanatory drawing in Text-figure 9D, 329.69, ×80.

Figs 3 and 6. *Ecchosis pulchribothrium* gen. et sp. nov. 3, patella, superior aspect, distal to left, explanatory drawing in Text-figure 9C, 411.19.96, ×65. 6, patella and proximal end of tibia, inferior aspect, distal to top, explanatory drawing in Text-figure 9B, 411.7.37, ×90.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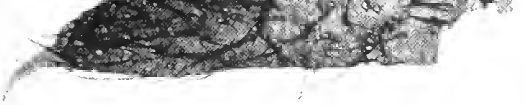
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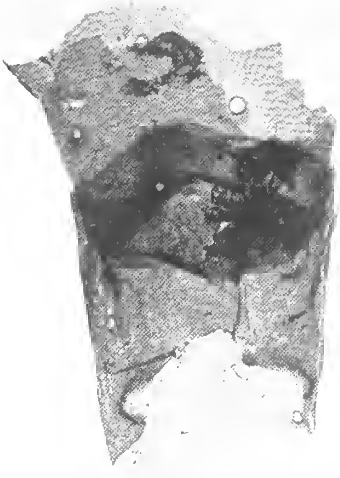
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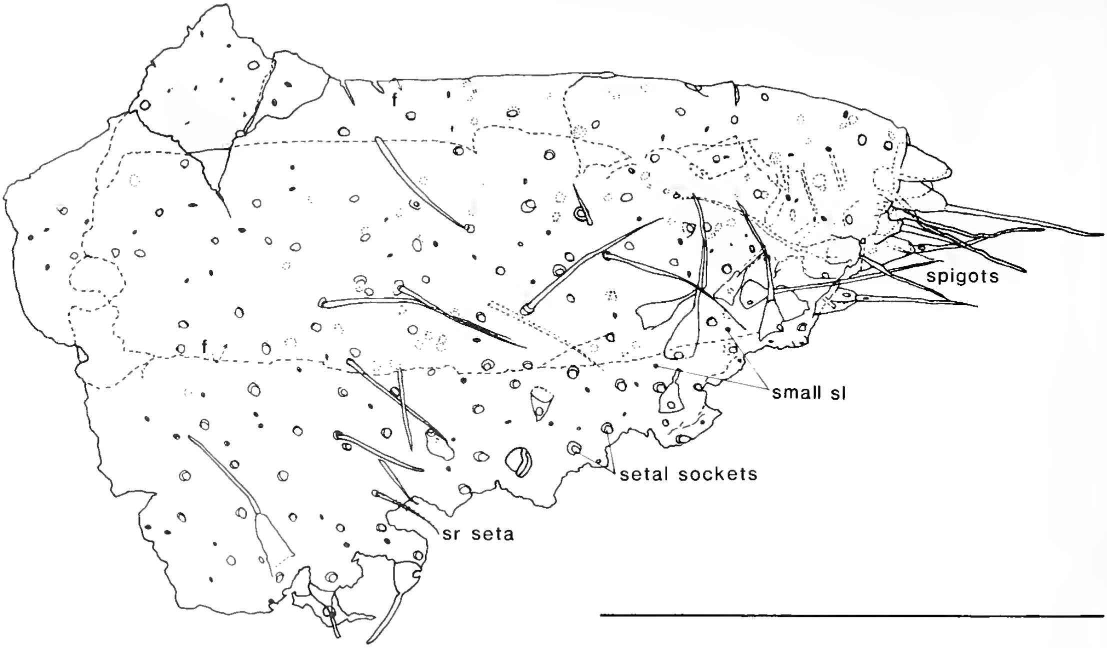


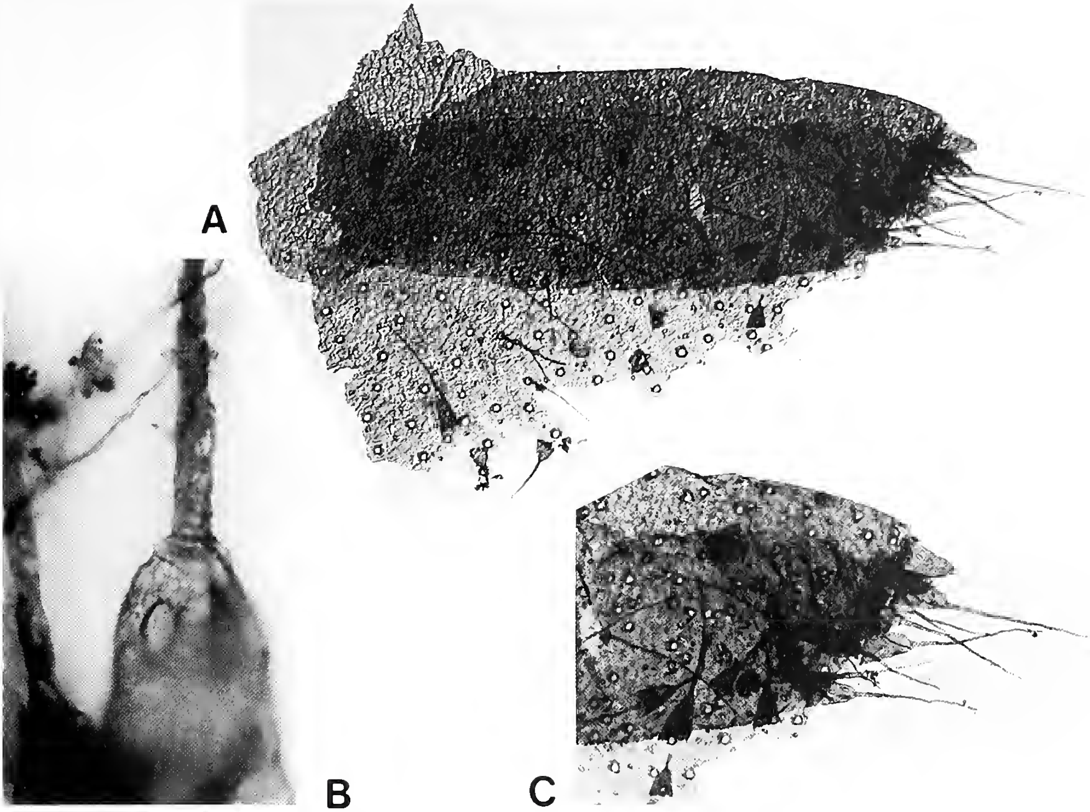
TEXT-FIG. 10. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawing for Text-figure 11, posterior median spinneret, distal to right, specimen is folded into three layers at thickest, small slit sensilla shown on near surfaces, setal sockets on far surfaces shown in dotted lines for clarity. Scale bar represents 0.5 mm; see MATERIAL AND METHODS for abbreviations and conventions.

inferiorly and inferodistally. The macrosetae are very prominent, see, for example, Plate 5, figure 3, and Shear *et al.* (1987, figs 132 and 133). A few slits are present inferoanteriorly and inferoposteriorly around the joint margin, adjacent to the macrosetae. No trichobothria have been seen on this podomere.

Tarsus. The tarsus (Pl. 5, figs 1–3, 5; Pl. 6, figs 1, 2, 4, 5) is about five-sixths the length of the metatarsus, and is similarly profusely clothed with two sizes of setae, and macrosetae occur inferiorly. Except proximally in larger specimens, the reticulate pattern characteristic of this genus is absent. The proximal joint bears two articulations which correspond to the articulations on the metatarsus. The leg tarsi are parallel-sided, and the distal joint bears three emarginations, in inferior, anterior, and posterior positions. Pairs of slit sensilla occur adjacent to the anterior and posterior embayments. There are three claws on the leg tarsi: the lateral claws are long and curved, the median claw is also quite long, and is thicker in mid-section and shorter than the lateral claws. All claws bear rows of fimbriae along their inferior edges (Pl. 5, fig. 1; Shear *et al.* 1987, figs 137–139). Trichobothria cannot be seen on any of the fossil specimens. A tarsal organ is present in a superodistal position (Pl. 5, fig. 1; Pl. 6, figs 2 and 4).

The palpal tarsus (Pl. 6, fig. 5; Shear *et al.* 1987, fig. 135) is not parallel-sided, but tapers distally and is also distinguished by the presence of only a single fimbriate claw.

Spinneret. The single spinneret (specimen 334.1*b*.34; Text-figs 10 and 11A–C), believed for reasons already discussed (Shear, Palmer *et al.* 1989) to be a posterior median spinneret, is about 0·94 mm long and represents a nearly complete single article of typical semifusiform shape. The specimen appears to have been torn along the median surface, and subsequently the torn edge (now nearest the observer as the spinneret is mounted on a microscope slide) was folded under itself. The cuticle is typical of *A. fimbriunguis*, ornamented with distinct polygonal cells, setal sockets and slit sense organs, the latter two structures densely but evenly scattered over the entire surface. Some of the sockets bear large, smooth setae, and a single serrate seta is present (Text-fig. 10). Spigots are scattered along the median surface only, and more densely clustered distally. Though folding and consequent superposition of structures makes an exact count difficult, at least 24 distinct individual spigots can be seen. There appears to be no significant variation in spigot size and form. Each spigot consists of a conical



TEXT-FIG. 11. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987). A–C, 334.1*b*.34. A, posterior median spinneret, distal to right, explanatory drawing in Text-figure 10, × 70. B, detail of base of lowermost, distally-directed, terminal spigot shown in A and C, with ?setal socket, distal to top, × 1200. C, distal end of spinneret showing detail of cuticle and spigots, × 130.

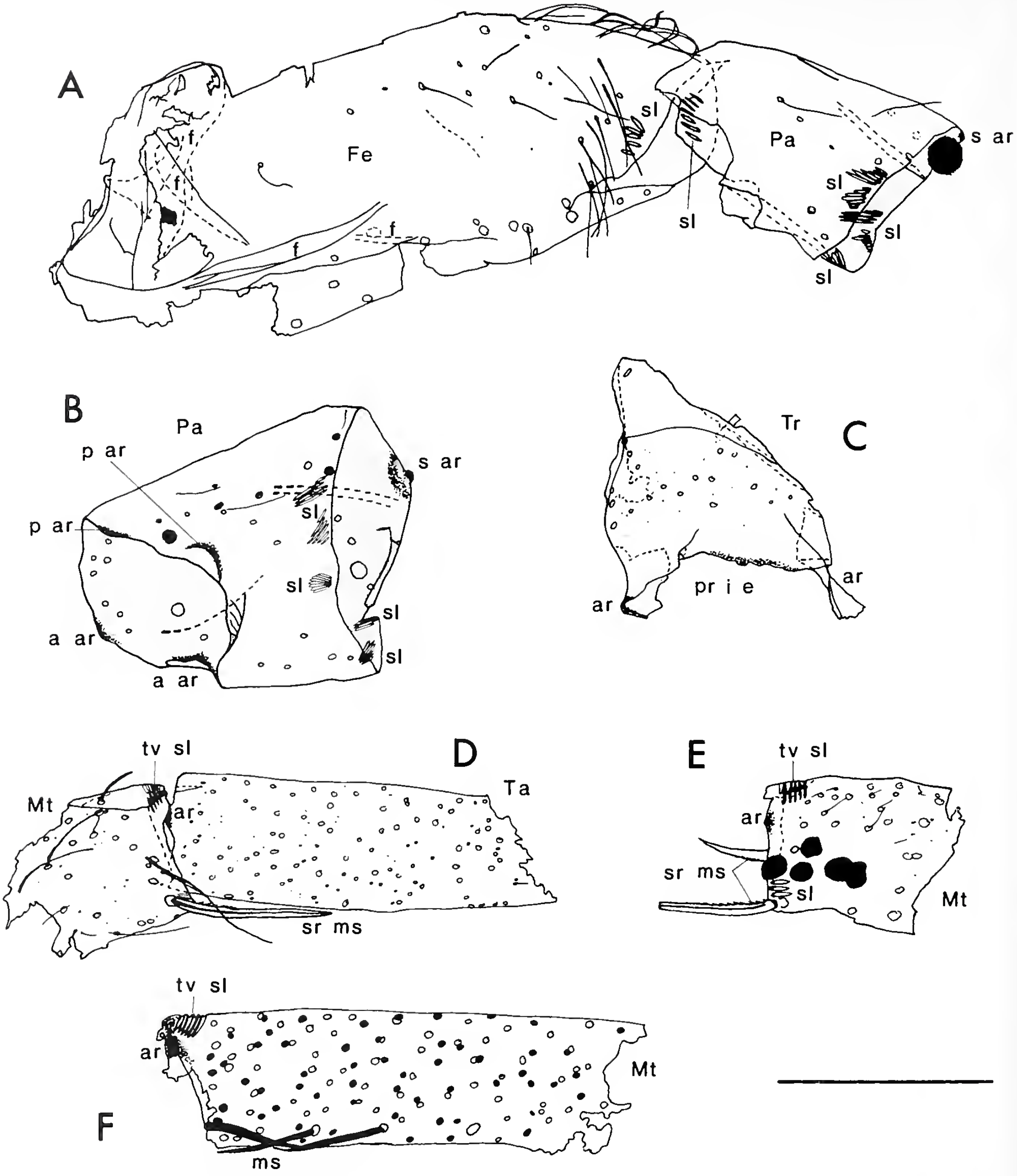
base approximately twice as long as wide, which narrows abruptly to a slender shaft no more than three times as long as the base. What appears to be a large setal socket is found on some of the spigot bases; the consistent position of this structure and careful focussing confirms that it is on the spigot base and is not a feature of overlying or underlying spinneret cuticle. The articulation of the base with the shaft is smooth, lacking a collar. No sculpturing is detectable on the distal part of the shaft, but extraordinarily fine sculpture, as is found on the shafts of some rastelloid mygalomorph spiders (J. Palmer, pers. comm.), may have been obliterated during diagenesis.

Subclass PULMONATA (*sensu* Firstman 1973) *incertae sedis*
Genus ECCHOSIS gen. nov.

Derivation of name. Greek, *ec-*, out of, from, and *chosis*, a heaping-up of earth; referring to the earth-dam for the pump-storage power station which now covers the Gilboa locality.

Type and only known species. Ecchosis pulchribothrium sp. nov.

Diagnosis. Pulmonate with patellar trichobothrium, the basal collar of which is ornamented with reticulate pattern of oval and lunate reticulate thickenings; thick, striated spines with bifid tips on some other podomeres.



TEXT-FIG. 12. *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987), explanatory drawings for specimens illustrated in Shear *et al.* (1987). A, 329.70, left walking leg femur and patella, anterior aspect, see Shear *et al.* (1987, fig. 129). B, 329.39, patella, inferior aspect, distal to right, see Shear *et al.* (1987, fig. 128). C, 329.59, trochanter, inferior aspect, distal to top, superior surface absent, specimen previously described and illustrated in Shear *et al.* (1987, fig. 140) as 'undetermined median structure'. D, 329.70, distal end of metatarsus and proximal tarsus, distal to right, setal sockets not differentiated according to surface and setae omitted from tarsus, see Shear *et al.* (1987, fig. 132). E, 329.70, distal end of metatarsus showing slit sensilla and serrate macrosetae, distal to left, setal sockets not differentiated according to surface, spores in black, see Shear *et al.* (1987, fig. 133). F, 329.57, distal part of metatarsus, distal to left, setae (except macrosetae) omitted, see Shear *et al.* (1987, fig. 131). Scale bar represents 0·5 mm for all specimens; see MATERIAL AND METHODS for abbreviations and conventions.

Ecchosis pulchribothrium sp. nov.

Plate 2, fig. 3; Plate 6, figs 3 and 6; Plate 7, figs 1, 3, 4, 7, 8; Text-figs 5C and 9B, C.

1987 Arachnida incertae sedis A, Shear, Selden and Rolfe; Shear *et al.*, pp. 70, 71, figs 146–150.

Derivation of name. Latin, *pulcher*, beauty, and *bothrium*, a cup.

Type specimens. Holotype: patella and base of tibia, on slide 411.7.37. Paratypes: patella? on slide 411.7.86; distal end of femur, on slide 411.1.33; two parts of unknown podomere with large sockets and striated spines, on slide 411.19.188.

Additional material. A complete list of the specimens referred to this species is deposited in the British Library, Boston Spa, Yorkshire, England, as Supplementary Publication No. SUP 14040, 5 pp.; see *Repository* above for availability of this publication.

Diagnosis. As for the genus.

Description

Cuticle. Large sheets of cuticle (Pl. 7, figs 1 and 7) of this animal occur in the Gilboa material, and are characterized by an ornament of small scales, resembling a reticulate ornament, thickened at one side, in which the connections between the thickenings have been lost. The scales are arranged in straight or arcuate parallel rows; the arcuate patterned cuticle is presumed to represent podomeres which have become opened out. The cuticle bears setal sockets whose diameters range in size from small (0·015 mm) to extremely large (0·15 mm), and additionally there are small (0·005 mm), circular pores scattered across the cuticle. The largest sockets only occur on one type of podomere. On what is presumed to be body cuticle, the setal sockets range up to 0·075 mm in diameter, and these larger ones commonly have a raised rim or broad spine on one side of the socket. This pattern is particularly emphasized on what are presumed to be edges of tergites, where a large thorn has a small spine articulated at its base; such an arrangement appears to be common on the cuticle of amblypygids. Large slit sensilla are also present on these pieces. The macrosetae are conspicuously striated, and the very large, thick spines are not only striated but also have bifid tips, a feature lacking on smaller setae (Pl. 7, figs 4 and 8). The cuticle of *Ecchosis* resembles that of *Liphistius* in the following features: scale-like sculpture, minute pores on cuticle surface, raised rim to larger setal sockets, and striations on macrosetae.

Coxa. The inferior surface and distal joint of the coxa is preserved on slide 2002.9.13 (Pl. 2, fig. 3). The costa coxalis can be seen to run as a thickened ridge towards the anterior dorsal edge of the podomere (which is not preserved). Close to the preserved proximal termination of the costa coxalis, and running at an angle from it towards the distal edge, is a folded piece of cuticle which is believed to represent the stiffened cuticle by which the coxa articulates dorsodistally with the body wall, in comparison with the coxa of *Liphistius*. The posterior and superior margins of the distal joint are folded across the anterior surface and the costa coxalis. The ventral surface is covered with setal sockets and richly supplied with pores; the inferoanterior surface bears fine setae. There is a fragment of the dorsal edge preserved at the proximal end of the podomere. No other specimen of this podomere is known.

Femur. A large femur is present on slide 411.1.33 (Pl. 7, fig. 1). Only the distal half is preserved, including parts of the distal joint: one of the articulations, a small group of slit sensilla adjacent and just superior to the articulation, and the emarginated inferior border. A number of small setal sockets are present, and two longitudinal rows of three or four larger sockets run along the inferior side of the podomere.

Patella. One definite patella is present, on slide 411.7.37 (Pl. 6, fig. 6), attached to the proximal end of a tibia. The patella is easily recognized by its emarginated inferior proximal edge, which bears inferoanterior and inferoposterior crescentic articulation points, for attachment of the arcuate sclerite (not preserved). The superior edge of the proximal joint is not preserved. The superior surface of the patella is twice the length of the inferior surface; it bears four or five setal sockets, some with setae, and a short distance proximal to the superior articulation of the distal edge lies an ornamented trichobothrial base. Three small slit sensilla occur between this bothrium and the articulation point, which is present at the extremity of the distally produced superior side of the distal joint. The inferior side of the distal joint is fairly straight, and is characterized by two groups of large slit sensilla, the slits at an angle distally diverging from the midline, and an inferiorly positioned single large slit which runs at an angle of about 80° from the others (this slit may be part of another group, but dark material obscures the podomere at this point). The presence of an inferior articulation at the distal joint is suspected, but not clearly seen because of the obscuring dark matter, because there is an articulation on the corresponding inferior side of the piece of tibia which is inserted into the patella (Pl. 6, fig. 6).

Two other podomeres bear an ornamented trichobothrial base. The best preserved specimen is 411.7.86 (Shear *et al.* 1987, figs 149 and 150). The bothrium consists of a ring of thickened cuticle surrounding a hole. Outside this ring is a collar of patterned cuticle which is more than three times the diameter of the hole. The pattern consists of a reticulum of thickened cuticle defining elliptical and lunate shapes. In the other specimens (411.7.37, 411.19.96) the morphology appears to be identical, as far as can be made out in these less well preserved examples. In no case is a hair seen emerging from the hole.

In the original description, the podomere bearing the well preserved example (411.7.86) was described as a possible femur because its distal end appears to have an inferior emargination (Shear *et al.* 1987, fig. 149). Now that the femur of *Ecchosis pulchribothrium* is known, it is certain that the earlier described podomere is not a femur. Specimen 411.7.86 could, however, be another patella. The bothrium occurs adjacent to the superior distal articulation; slit sensilla may be present on the emarginated inferior side of the distal joint, but could not be seen because of the folding (Shear *et al.* 1987, fig. 149). Both the inferior side and the proximal joint are not well preserved in 411.7.86; it is uncertain whether this specimen represents a different podomere with the same kind of trichobothrial base, or another patella.

The third specimen bearing an ornamented trichobothrial base (411.19.96, Pl. 6, fig. 3) resembles a trochanter at first sight; closer inspection, however, reveals that it has been proximodistally compressed to some degree, and the proximal joint is incompletely preserved. It, too, could be a patella. The preserved inferior surface is short, and bears three groups of slit sensilla. Two of these are situated close to the inferior articulation (which is not strongly developed), and they diverge distally at an angle from the midline. The other group diverges at an 80° angle from the first two groups, and is situated on the other side of the midline from them. The trichobothrial organ is obscured by folding; it is situated, like those on the other two podomeres, a short distance behind and a little to one side of the superior distal articulation.

Tibia. Only the fragment attached to the patella in 411.7.37, described above, is known with certainty. This piece has superior and inferior proximal articulations. It is interesting in that its lateral sides appear to diverge distally; possibly it was a tumid podomere in this leg in life. In addition, a number of examples of a long podomere with extremely large setal sockets occurs among the specimens; 411.19.188 (Pl. 7, fig. 8) and 329.46 are good examples. The proximal end of the podomere does not occur on any of these specimens, but these podomeres are at least three times as long as wide, and have two rows of large sockets, each row with at least 8 sockets, along their length. In addition to the rows of major sockets, there are about 10 rows of smaller setal sockets running along the length of the podomere. There is commonly a smaller seta adjacent to each major socket. The large sockets bear thick, spindle-shaped movable spines, each about four times as long as maximally wide in the compressed state. The spines have straight striations running along their length, are

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EXPLANATION OF PLATE 7

Figs 1, 3, 4, 7, 8. *Ecchosis pulchribothrium* gen. et sp. nov. 1, inferodistal part of femur, inferior to top, distal to right, showing cuticle sculpture, 411.1.33, × 53. 3, part of distal joint of unknown podomere showing slit sensilla grouped into lyriform organ, 411.19.184, × 72. 4, thick, striated, bifid spine on unknown podomere, 411.19.137, × 53. 7, patch of cuticle (part of body not known) showing cuticle sculpture, 411.19.206, × 89. 8, superodistal part of unknown podomere showing cuticle sculpture, setae, spine and their sockets, and lyriform organ, 411.19.188, × 118.

Figs 2 and 6. Extant amblypygid *Heterophrynus elaphus*, specimens cleared in potassium hydroxide. 2, trichobothrial base adjacent to superior articulation at distal joint of tibia 4, × 135. 6, left chelicera, ectal aspect, dense setation around teeth removed for clarity, transmitted light under ethanol on Olympus SZH stereomicroscope, × 7·5.

Fig. 5. Extant uropygid *Mastigoproctus giganteus*, left chelicera, mesal aspect, specimen cleared in potassium hydroxide, dense setation around teeth removed for clarity, transmitted light under ethanol on Olympus SZH stereomicroscope, × 7·5.

PLATE 7


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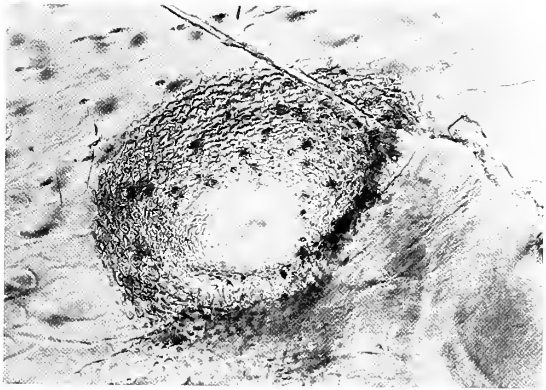
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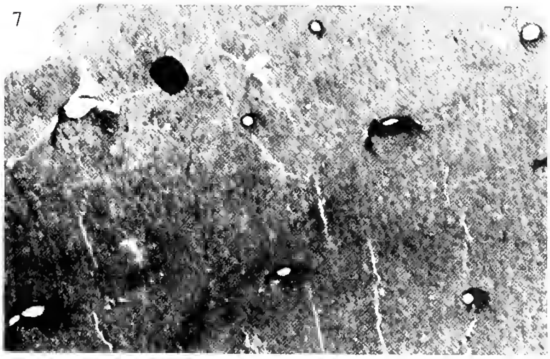

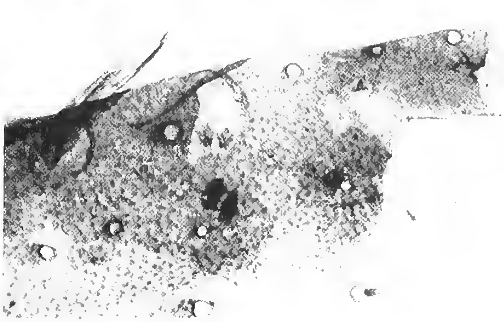
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SELDEN *et al.*, *Ecchosis*, *Mastigoproctus*, *Heterophrynus* broad at the base, and have a bifid tip (Pl. 7, fig. 4). The normally shaped macrosetae present on the podomeres are also striated, and do not have bifid tips. The smallest setae are relatively short. The distal end of one podomere is preserved (Pl. 7, fig. 8), and shows a longitudinal lyriform organ.

There is no conclusive evidence of the identity of these large podomeres. The short trochanter and patella, and the terminal tarsus can all be ruled out. Of the long podomeres, all pulmonate metatarsi have a lyriform or group of slit sensilla at the distal end, in which the slits are aligned transversely. Pulmonate femora bear rows of slit sensilla rather than lyriforms, characteristic articulation points, and are normally distinctly emarginated. It is therefore most likely that the long podomeres represent tibiae. Well developed lyriform organs occur on the distal ends of the tibiae of spiders, but not of amblypygids or uropygids (Barth 1978, fig. 3).

Discussion. Is the ornamented sense organ, which is one of the characteristics of *Ecchosis*, a true trichobothrium? Among living arachnids, the trichobothrium is fairly widespread, occurring in all groups except Ricinulei, Solifugae, and Opiliones. Ornamented trichobothrial bases are known from living spiders, although none has the same type of pattern see in *Ecchosis*. It is also rare to find a trichobothrium on the patella of an arachnid; they occur more commonly on the more distal podomeres of the legs. A literature search for spiders with patellar trichobothria revealed none, and R. Forster (pers. comm.) is aware of no spider with patellar trichobothria. However, a study of specimens of other Pulmonata revealed that whereas uropygid patellae bear no trichobothria, they are present on the patellae of legs 2, 3, and 4 of Amblypygi. Weygoldt (1972) described two trichobothria on each walking-leg (2, 3, 4) patella of all species of *Charinus*, and we observed this same pattern on *Heterophrynus elaphus*. Quintero (1980) described these organs on the patella of *Acanthophrynus coronatus*, and called them 'campaniform sensilla', but they do not seem to differ in morphology from the tibial trichobothria. They bear a fine hair emerging from the central hole, as drawn by Quintero (1980, fig. 6) and so are not campaniform sensilla. Of especial interest is the ornamentation of the collar (Pl. 7, fig. 2); it is remarkably similar to that observed in *E. pulchribothrium*, and quite different from that on the trichobothria found on uropygids and spiders. The patella of amblypygids is different in shape from that of *E. pulchribothrium*, being specialized for immobility and twisted to enable the crevice locomotion of these bizarre animals (Manton 1977), so that whilst their patellar trichobothria lie adjacent to the superior distal articulation, this articulation is situated in a triangular notch in the distal edge of the podomere.

It is therefore possible that *Ecchosis* is an amblypygid, but without additional evidence, the genus cannot be assigned to that group. It is probable that in the Devonian there were Pulmonata with a mosaic of characters which today are found in separate taxa.

Class ARACHNIDA Lamarck, 1801 *incertae sedis*

Plate 5, figs 3 and 4

Five specimens (329.60, 329.62, 334.1*a*.4, 411.2.4, 2002.9.20: Pl. 5, figs 3 and 4) of lengths of short segments are present in the Gilboa material. The segments are about one and a half times as long as wide and all are virtually identical, apart from the terminal one in some specimens. No more than 12 occur together. Each has a distal collar into which the next succeeding segment is inserted, and this collar bears setal sockets all round. The cuticle is patterned with transversely elongate reticulate sculpture, and scattered across the surface are some small pores which resemble the little slit sensilla of *Attercopus* (they differ slightly, however, in that these always appear eliptical or lunate even at low magnification). The setae are very long and thin, and do not have bifid tips (there are many specimens of another type of flagellar appendage in which the segments are about three times as wide as long, in the compressed state, in which the setae have bifid tips with branches of different lengths). There is no evidence to link these flagellar appendages with any arachnids, except that the little pores, if they are slit sensilla, would confirm an arachnid rather than any other arthropod group. These organs might be the caudal flagellum of a uropygid (and evidence is amounting that *Gelasinotarbus bonamoae* may prove to be one of these animals) or could be the flagelliform first leg of an amblypygid. Similar antenniform appendages with slit sensilla have also been found in Stephanian deposits from Kansas (A. J. Jeram, pers. comm.).

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ORDOVICIAN GRAPTOLITES FROM THE EARLY HUNNEBERG OF SOUTHERN SCANDINAVIA

by KRISTINA LINDHOLM

ABSTRACT. A graptolite fauna of Early Hunneberg age is described from southern Scandinavia (Scania, Västergötland, Oslo region). Correlation and boundaries within the interval are discussed and it is suggested that the Hunneberg Stage be elevated to series rank, interposed between the Tremadoc and the Arenig. One new dichograptid genus, *Hunnegraptus*, and three Scandinavian representatives of it, *H. copiosus*, *H. tjernviki*, and *H. robustus*, are erected. The genus is multiramous, with long first-order stipes, and shows presumed rejuvenation of gerontic specimens. It is likely to be most closely related to *Clonograptus*. Six additional species are formally named: *Kiaerograptus supremus* (Anisograptidae), *Clonograptus (C.) magnus*, *Tetragraptus longus*, *T. krapperupensis* (Dichograptidae), *Paradelograptus elongatus*, and *P. tenuis* (Sinograptidae). The sequence containing these taxa is divided into three zones: the *K. supremus* Zone which probably starts in the Late Tremadoc, the *A. murrayi* Zone, and above that the *H. copiosus* Zone, which underlies the Late Hunneberg *Tetragraptus phyllograptoides* Zone. The fauna covers part of the interval when anisograptids gave way to graptolites of the dichograptid development stage, and the observed steps in this evolution (loss of bithecae) are described.

GRAPTOLITES from the Upper Tremadoc and Lower Arenig of southern Scandinavia have been known for over a hundred years, e.g. Tullberg (1880), Holm (1881), Brøgger (1882), Herrmann (1883, 1885), Törnquist (1901, 1904), Strandmark (1902), Monsen (1925, 1937), Spjeldnaes (1963), and Erdtmann (1965*a*). Yet, the fauna described in this paper, which comes from a 'post-Tremadoc, pre-Arenig' level, remained unrecognized until Tjernvik (1956) made his overview of the Lower Ordovician of Sweden. From a darker band in a grey shale unit at Storeklev, at Mt Hunneberg (Text-fig. 1A), he mentioned a few peculiar graptolites, which he referred to as 'undescribed dichograptids' in his correlation table. No description of this fauna has been given to this day. The fauna, together with several accompanying species, was later found in lithologically similar beds in the Oslo region, mainly by N. Spjeldnaes in the Slemmestad area and by B.-D. Erdtmann in central Oslo. More recently, I re-collected both the Storeklev and the Slemmestad localities. Finally, I identified the fauna, and also older post-Tremadoc graptolites, in a grey to nearly black shale sequence in the Krapperup drillcore in NW Scania. The rarity of identifiable graptolites in the basal beds of the core and absence of the otherwise ubiquitous Ceratopyge Limestone make lithostratigraphic and chronostratigraphic correlation of these basal beds difficult. Judging by circumstantial evidence, however, all of the basal beds probably belong to the Hunneberg.

From my own observations in the Lower Ordovician of southern Scandinavia (Lindholm 1991), a closely similar sequence of facies and faunas is developed in the Oslo region, Mt Hunneberg in Västergötland, and SE Scania. All areas can be regarded as lying within a single confacies belt, equivalent to Jaanusson's (1976, 1982) Scanian and Oslo confacies belts, at least until the end of Arenig time. They undoubtedly represent a single, original depositional basin which included, as a thicker and further offshore facies, the NW Scanian sequence of the Krapperup bore core.

All three areas, Oslo, Mt Hunneberg, and Krapperup, have been cut by various forms of late Carboniferous to early Permian intrusives. In other respects, the geological settings of the three areas, as seen today, differ due to their later geological history. The Oslo region is a large, more or less continuous area of well exposed Cambrian to Silurian sediments close to the Scandinavian fold

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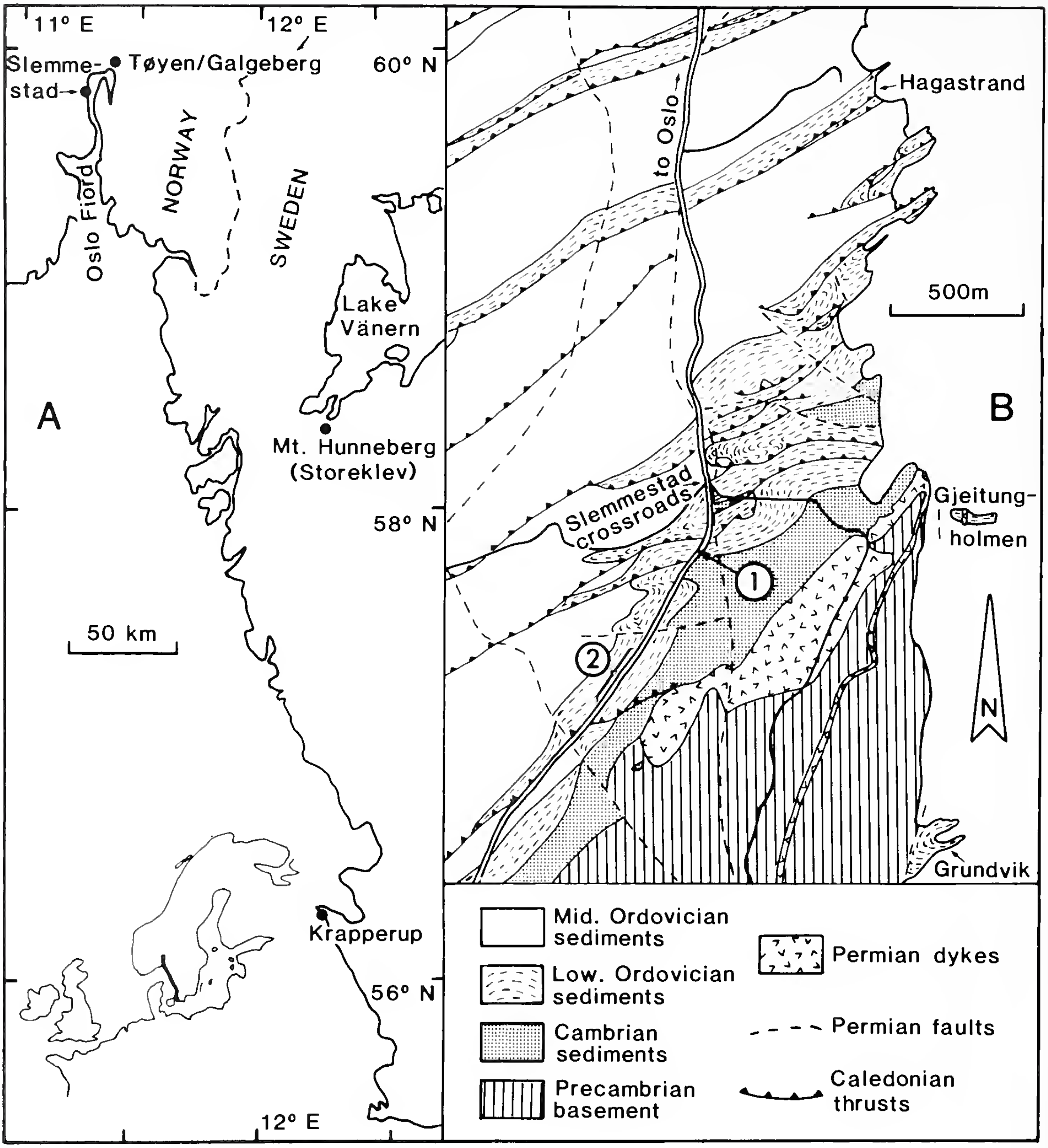


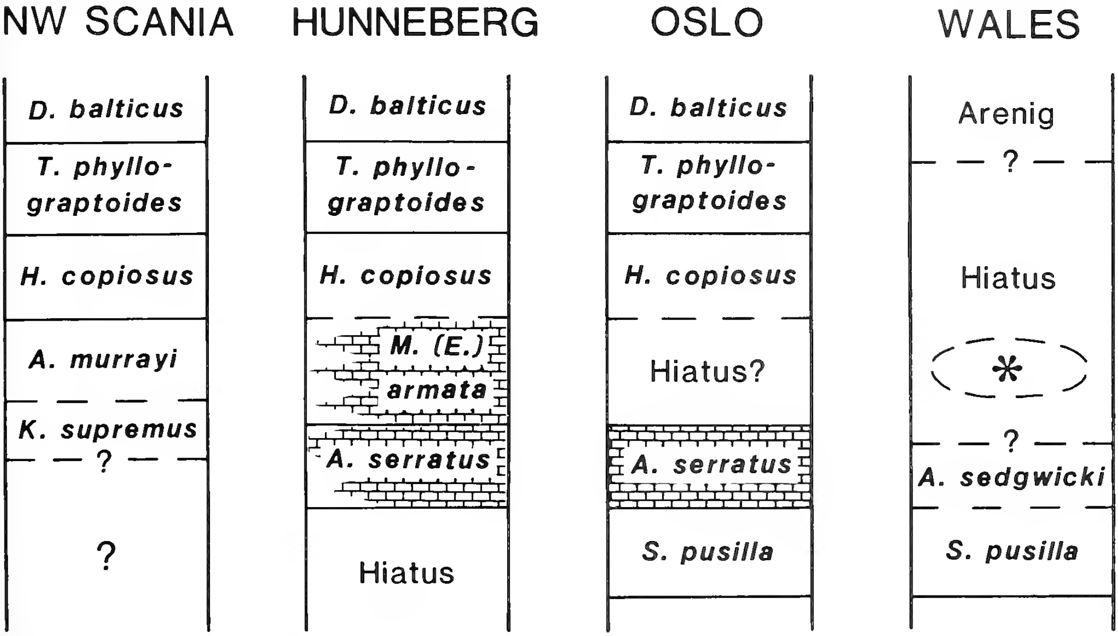
TEXT-FIG. 1. Location of the study area. A, Outline map showing location of investigated localities. B, Detail map of the Slemmestad area, showing the structural complexity; redrawn from Bockelie (1982). The main sampling localities of Lower Hunneberg rocks were the coastal sections at Grundvik and Hagastrand, a road-cut just south of Slemmestad crossroads (eastern side of the road), the new standard section (1; western side of the road), and a long continuous roadside exposure (western side) marked '2'. This is the 'Rortunet' section (Bødalen or Buss-stop Nybygget of previous collectors), which is most complete stratigraphically at its southern end. It is cut by a couple of minor thrust faults and Permian dykes. South of area '2' is another roadside exposure (western side), partly hidden behind trees. This section is the *Kiaerograptus* locality of Spjeldnaes (1963) which, however, also contains Hunneberg age beds. In addition, a few samples are labelled with street names, and one sample derives from the islet Gjeitungholmen.

belt. The beds are gently, to somewhat more complexly, folded, with minor associated thrust faults particularly in the Slemmestad area where structure can be easily observed (Text-fig. 1B). Mt Hunneberg, on the other hand, constitutes a very small, isolated but well exposed area of Cambrian and Lower Ordovician sediments on a Precambrian basement, protected by a thick dolerite cap. The beds are flat-lying. Finally, the Krapperup area (NW Scania) is a small (1 × 7 km) fault-bounded block, surrounded by Mesozoic rocks, and lying within a zone of intense block faulting, the individual blocks of which are sometimes less than 1 km in width. The NW Scania area forms part of a broad tract of discontinuous outcrops, extending from NW to SE Scania, of Lower Palaeozoic rocks. The beds, and graptolite faunas described here, however, are known only from the western part of Scania.

STRATIGRAPHY

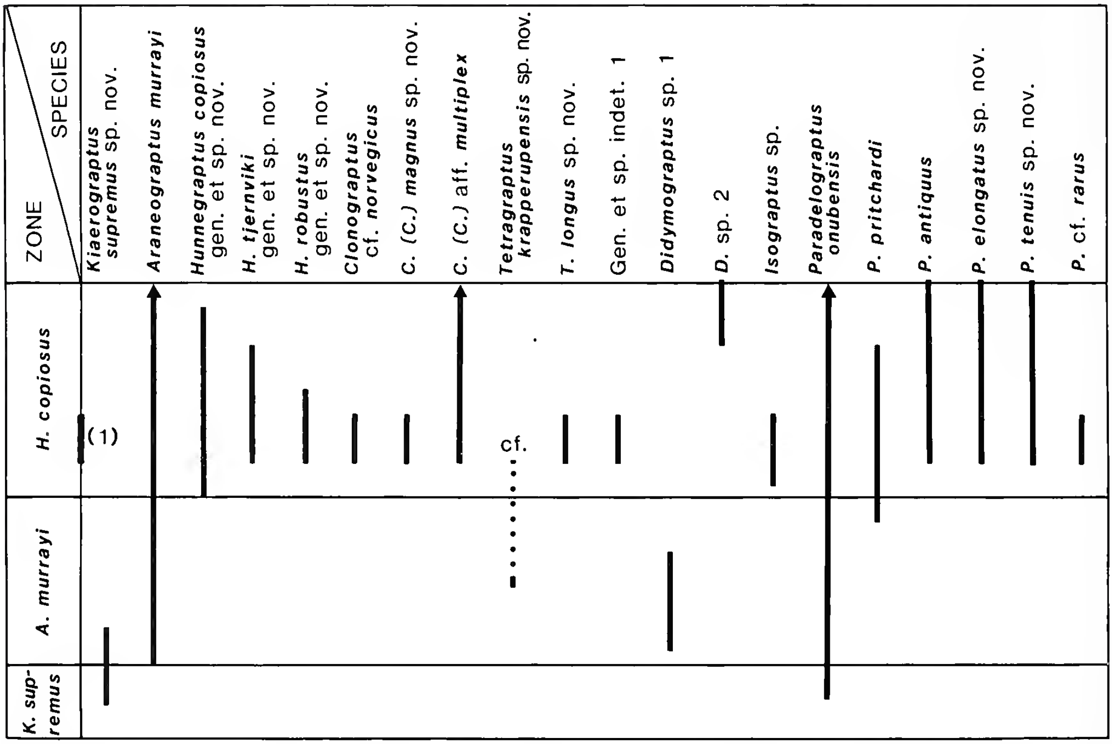
Zonation of the sequence. In Scandinavia, the interval from the base of the Ceratopyge Limestone to the base of the *T. phyllograptoides* Zone (roughly corresponding to the faunas described herein) has not formally been divided into graptolite zones; a '*Didymograptus? stoermeri* Zone' was indicated by Erdtmann (1965*b*, text-fig. 5; not defined in text) for the time interval spanning the Ceratopyge Limestone, but based on finds from the very top of the unit only (Erdtmann 1965*a*, p. 108). The same graptolite fauna is also present in W. Scania, in the Fågelsång core (Hede 1951; '*D. balticus*' Zone, followed by a major hiatus). Here, *D.? stoermeri* is found well above the Ceratopyge Limestone. The species was not found in the Krapperup core, despite examination of every cm of the lowermost metres of the core, nor was anything else as primitive-looking.

I propose a subdivision, based on the Krapperup core sequence, into (Text-fig. 2): a *Kiaerograptus supremus* Zone (Krapperup core, 155·06 m (base)–148·22 m); an *Araneograptus murrayi* Zone (148·22 m–132·73 m); and a *Hunnegraptus copiosus* Zone (132·73 m–112·80 m). The base of the *K. supremus* Zone corresponds to an undefined level within the Ceratopyge Limestone. The bases of the *A. murrayi* and *H. copiosus* Zones are defined by the incoming of their zone fossils. The base



TEXT-FIG. 2. Attempted correlation of part of the Lower Ordovician between Scandinavia and Wales. The lithologies are clastic, except where indicated; * shows stratigraphic position of beds described by Molyneux and Dorning (1989).

of the overlying *T. phyllograptoides* Zone is defined by the incoming of *T. phyllograptoides* or a considerable increase in horizontal and reclined tetragraptids, whichever comes first, and roughly corresponds to the base of the *T. approximatus* Zone elsewhere. The approximate distribution of species is shown in Text-figure 3.



TEXT-FIG. 3. Summary of observed ranges of taxa present in topmost Tremadoc to Lower Hunneberg beds in southern Scandinavia. (1) indicates estimated relative position of the graptolite-rich horizon at Mt Hunneberg and in the Oslo region.

The case for a Hunneberg Series. It has long been known (e.g. Skevington 1966) that there is a sizeable hiatus between the Tremadoc and the Arenig in their respective type areas in Wales. The fauna described herein, of Hunneberg age, fits into this hiatus. Also, there is no general agreement yet as to where to put the boundary between the Tremadoc and the Arenig. This uncertainty concerns mainly beds of an age corresponding to La 2–La 3 in the Australasian stratigraphic scheme, and sometimes also beds of Be 1–Be 2 age (e.g. Rushton 1985). As things stand, the Hunneberg interval can thus be regarded in four different ways:

1. as a series filling the gap between the Tremadoc and the Arenig;
2. as the basal stage of the Arenig;
3. as the topmost stage of the Tremadoc;
4. as part Tremadoc, part Arenig.

The trend is nowadays towards a reduction of the number of series, e.g. the suggested amalgamation of the Llanvirn and the Llandeilo. Still, I am in favour of the introduction of a new Hunneberg Series, interposed between the Tremadoc and the Arenig, as previously suggested by Erdtmann (1988). In my opinion, this is the easiest way round a difficult problem. Even from the British point of view, it would be an advantage: what now is Tremadoc and Arenig in their respective type areas would remain so, whereas the beds of 'uncertain' age in the Lake District and

South Wales described by Rushton (1985), Molyneux and Rushton (1988), and Molyneux and Dorning (1989) would belong to the Hunneberg. The beds described in the above papers are all of La 2 age. My examination of the graptolites described by Molyneux and Rushton (1988) and comparison with Scandinavian and Spanish material proves them to be considerably older than the *T. approximatus* Zone (La 3).

I would recommend a Hunneberg Series of the extent originally suggested by Tjernvik (1956), not the revised concept of Tjernvik and Johansson (1980) who referred the topmost zone, that of *D. balticus*/*M.* (*V.*) aff. *estonica* ('Transition beds'), to the overlying Billingen Stage. It seems that the most practical definition of the Hunneberg Series would be in terms of conodonts, as comprising the conodont zones of *P. proteus* and *P. elegans*. This would closely fill the Tremadoc/Arenig hiatus in the type areas. The base of the Hunneberg would correspond to the Scandinavian top of the Tremadoc, however, which is equivalent to a level higher than the top of the Tremadoc in its type area in Wales (Skevington 1966; Henningsmoen 1973). From elsewhere in Wales and adjacent areas, Rushton (*in* Whittington *et al.* 1984) mentions younger beds which he refers to the Tremadoc. He includes a trilobite fauna correlated with the *Shumardia pusilla* Zone of Scandinavia which (Regnéll 1960) lies within the Ceratopyge Shale, and a younger *Angelina sedgwicki* Zone fauna which cannot be correlated with Scandinavia. Therefore, beds equivalent to the Scandinavian topmost Tremadoc *Apatokephalus serratus* Zone (Ceratopyge Limestone) are not definitely known in Wales. An approximate correlation between the Scandinavian and Welsh faunas is given in Text-figure 2.

The top of the graptolite sequence here described is considerably older than the oldest graptolite fauna in the type area of the Arenig. That fauna was described by Zalasiewicz (1986) and corresponds to a level no lower than the upper part of the *D. balticus* Zone or more probably the *P. densus* Zone of Scandinavia (Lindholm 1991). According to Fortey and Owens (1987, p. 99) no strata of *Tetragraptus approximatus* Zone age have been proven to exist in Wales, although they suspect rocks equivalent in age to the upper part of the zone to be present. All of the graptolite fauna described herein appears to be older than the *T. approximatus* Zone.

Cooper and Lindholm (1991) have made an attempt at estimating the relative duration of the different intervals in the Early Ordovician. That study indicates that the duration of the Hunneberg Series, as proposed here, is longer than the Tremadoc, taken as the *Rhabdinopora flabelliformis desmograptoides* Zone – *Apatokephalus serratus* Zone (the Scandinavian concept). It is only slightly shorter than the 'remaining' Arenig and of approximately equal length to the combined Llanvirn–Llandeilo. A further argument for a Hunneberg Series is the disagreement between workers on different fossil groups if the beds in question are 'Tremadoc' or 'Arenig' in age. Graptolite workers have generally considered the 'La 2' beds as 'Tremadoc', whereas conodont workers, working in different facies, call coeval beds 'Arenig'. It should be noted here that the base of the conodont zone of *P. proteus* lies considerably lower than the base of the *T. approximatus* Zone, contrary to the views of Barnes *et al.* (1988) (Löfgren in prep.). Different graptolitic facies have been treated equally ambiguously (Lindholm 1984): typical La 2 beds have been referred to the Tremadoc, whereas the coeval *A. murrayi* beds have been considered to be of Arenig age (e.g. Thoral 1935; Destombes *et al.* 1969). The works of Williams and Stevens (1991), Stouge and Bagnoli (1988) and Löfgren (in prep.) have added to the precision in correlation between the graptolite and conodont zonation. According to conodont evidence, the lower part of the La 2 graptolite fauna is of Tremadoc age (that described by Williams and Stevens (1991) from Newfoundland) whereas higher parts (this work) belong to the *P. proteus* conodont zone, generally regarded as of Arenig age.

LOCALITIES

In Scandinavia, the Lower Hunneberg beds outcrop only in the Oslo region (east-central Oslo and Slemmestad) and at Mt Hunneberg. In Scania they are known only from the Krapperup core, the basal beds also from the Fågelsång core (*D. balticus* Zone of Hede (1951)). Based on lithological similarity, they appear to be present both further to the south (SE Scania) and to the north (Hamar at Lake Mjosa). These beds are, however, unfossiliferous.

The only graptolite-bearing outcrop of Lower Hunneberg beds at Mt Hunneberg is at Storeklev, in the south-west wall of the mountain. Here, the Lower Hunneberg is represented by shale, and is thicker than elsewhere. The sequence gradually thins and shale gives way to limestone towards the eastern wall of the mountain. At Storeklev, graptolites are found scattered through the lower part of the shale, within which there is one rich band, 2·15–2·32 m above the hiatus separating the Cambrian from Ordovician beds (Tjernvik 1956). The collections investigated from Storeklev consist of T. Tjernvik's original material (PU Vg 124–127), B.-D. Erdtmann's collections from the early 1960s (TUB HUN-S/2.18–2.3/001-058) and my own collections from 1979–1986, belonging to Lund University.

The Oslo region, *c.* 200 km north-west of Mt Hunneberg, contains several outcrops of Lower Ordovician graptolite shale, but the Lower Hunneberg beds are found only in the central part, at Galgeberg and Tøyen (both in east-central Oslo) and in the Slemmestad area (*c.* 20 km south-west of the Oslo localities). The Galgeberg and Toyen localities were temporary construction sites, and are now inaccessible, whereas the Slemmestad area contains several well-exposed localities (road sections and beach sections; Text-fig. 1B). My own collecting at Slemmestad has shown the graptolites to be less rare than at Storeklev, but at both localities there are unusually rich horizons. The collections investigated from the Oslo region consist of material from Galgeberg collected in the 1930s by T. Strand and A. Heintz (PMO 58.965–58.970); B.-D. Erdtmann's collection from the Tøyen underground station (GPI T1–T30; PMO 73.652); collections from various localities in the Slemmestad area, mainly by N. Spjeldnaes, to a minor extent by G. Henningsmoen and D. Bruton (PMO 137, 73.187–73.192, 73.200, 73.204, 97.702, 97.705–97.706, 97.708, 108.557–108.574, 108.598–108.599, 112.966–112.970, 113.031–113.033, 120.751); and finally, my own collections from various localities in the Slemmestad area – the most productive one being Grundvik between Slemmestad and Naersnes to the south. My collections are all measured in sections, and belong to Lund University.

The investigated part of the Krapperup core (situated *c.* 230 km S of Mt Hunneberg) consists of the lowermost *c.* 42 m (155·06–112·80 m), comprising the Lower Hunneberg beds. 193 samples, not all of which contained identifiable graptolites, have been taken out of this part of the core. The core was drilled in the 1940s and belongs to Lund University. Its diameter is 62 mm.

All the material examined consists of medium grey to almost black, non-calcareous, shale/mudstone. The preservation of the graptolites varies from flattened to full relief, infilled with pyrite or, commonly in the lowermost part of the Krapperup core, with calcite. In the latter case, the periderm is usually very brittle and partly flakes off during splitting of the slab or preparation. Also, some of these graptolites were partly compressed and deformed before infilling with calcite. They are, consequently, often hard to identify.

GRAPTOLITE TERMINOLOGY

The terminology in general follows that of Bulman (1970) and Cooper and Fortey (1982, 1983; isograptid development type, dextral and sinistral mode, consecutive and delayed dichotomies etc.). Didymograptid and tetragraptid proximal part refers to the length of first-order stipes (several *vs.* one theca each). Profile stipe width refers to measurements made from the dorsal edge of the specimen to the ventral wall of a theca, at its aperture – the aspect of the stipe is referred to as 'profile view'. Lateral stipe width refers to specimens in dorsal or ventral view ('dorsoventral view'; horizontal preservation of multiramous specimens), that is, measurements are made from side to side of the stipe. The number of thecae in 10 mm has usually been measured over the available number of thecae, and then recalculated. Stipe divergence angles are measured as the angle resulting from the tangents of the dorsal side of the stipes across a specified thecal aperture. Secondary cortex cover in general refers to what appears to be an 'envelope' around the stipe, compressed to a film in the bedding plane in an arbitrary preservational aspect of the specimen; only exceptionally does the cortex cover appear to have thickened the stipe into a robust 'rod'. The terms sicular bitheca and plaited thecal structure are explained in the section on evolution. Dichograptid stipe indicates a stipe without triad budding or plaited thecal structure, i.e. 'fully graptoloid'. Graptoloid thecal notation is used throughout.

In the systematic section, the suprageneric classification of Fortey and Cooper (1986) has, in general, been followed (see discussion on the Sigmagraptinae, however). In the synonymy lists the signs recommended by Matthews (1973) have been used. Under the heading of 'Associated species' are listed only the species found on the same bedding plane as the species under discussion.

EVOLUTION AND PHYLOGENY

The fauna discussed in this paper represents a stage in graptolite evolution when (along various lineages) biradiality had generally been attained and bithecae were in the process of being lost. The coexistence of sinistral and dextral forms of a species is a common feature in early Hunneberg time. The fauna does not verify any general trend towards reduction in the number of stipes present in a rhabdosome.

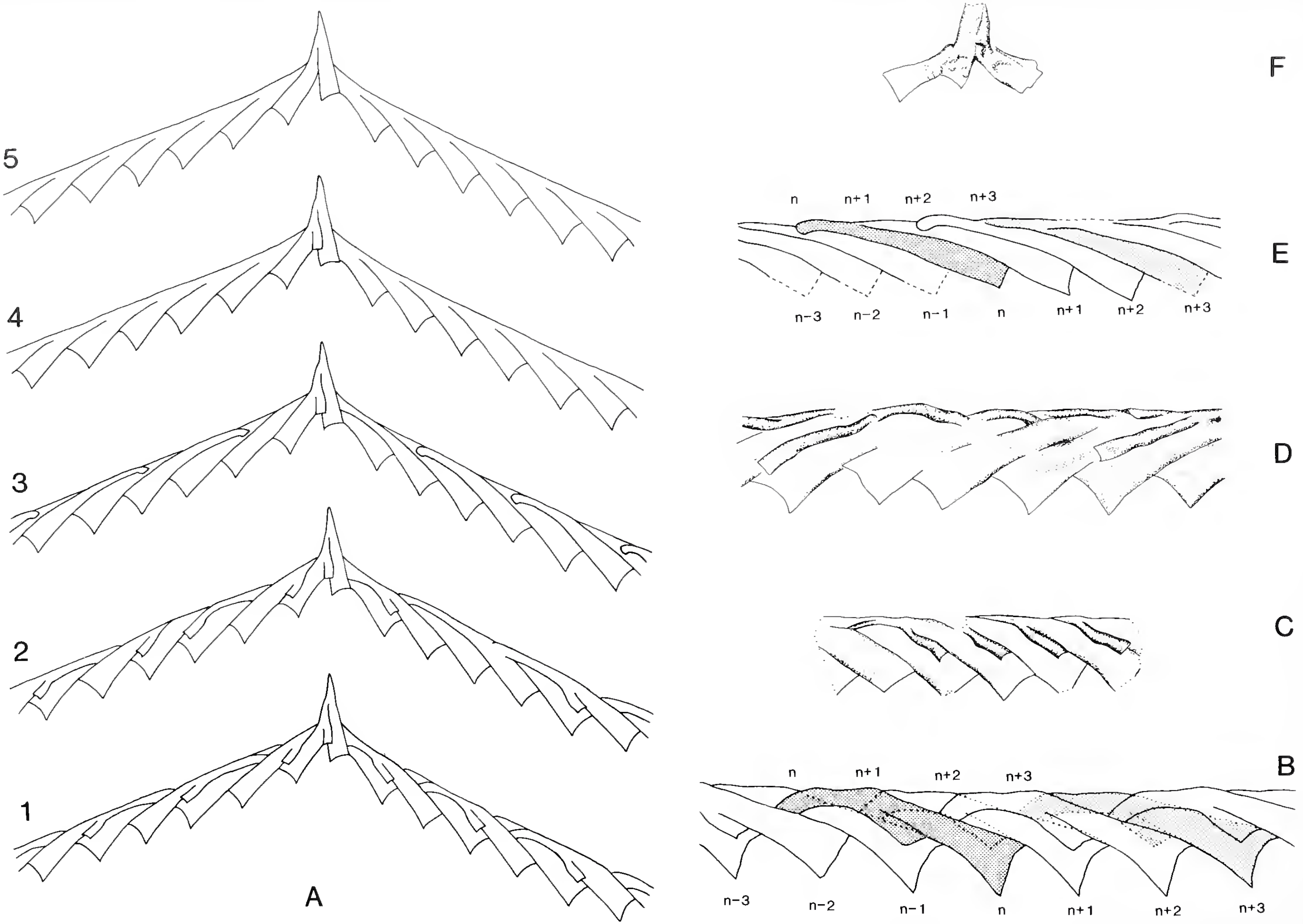
Loss of bithecae. Bithecae were lost along different lineages in a rather restricted time period, Late Tremadoc and Early Hunneberg. Late Tremadoc graptolites showing various degrees of bithecal reduction were described by Williams and Stevens (1991).

I have not been able to verify if the various steps in this transformation follow in the same order (homotaxially) in different groups, nor if bithecae were lost progressively along a stipe or instantaneously. I have seen a limited number of combinations of primitive and advanced traits (Text-fig. 4A) that can be listed as five steps in a morphological series:

1. The typical anisograptid: a fully bithecate rhabdosome, with normal triad budding, i.e. successive groups of one autotheca, one bitheca, and a stolotheca, produced at stolonal nodes. These groups alternate regularly (Bulman 1970, fig. 8), so that, from one side of the rhabdosome, only every second bitheca can be seen (Text-fig. 4A: 1, B). In profile view, the thecae are seen to bud laterally (Text-figs 4C, D, 5A, B). The alternation is seen as a zig-zag or sinuous pattern in dorsal view.
2. A fully bithecate rhabdosome with irregularities in the triad budding, that is, two or more successive bithecae may be present on one side of the rhabdosome (Text-fig. 4A: 2, C, D), e.g. *Kiaerograptus supremus*.
3. Only a sicular bitheca is present, i.e. the bitheca associated with th 1^1 and present between the sicula and th 1^1 on the obverse side. The stipes have traces of triad budding, here termed *plaited thecal structure*. The name has been chosen to illustrate the zig-zag or sinuous path of the common canal, as seen in dorsal view, caused by the fact that the thecae still alternate, even though the bithecae have been lost (Text-fig. 4A: 3, E), and their proximal parts produce a 'herringbone' or plaited structure (in dorsal view). The budding is closer to the dorsal side of the rhabdosome than in the bithecate species examined, suggesting the possibility that the transition from lateral to dorsal budding was a gradual one.
4. The sicular bitheca remains, but the stipes are of normal dichograptid appearance (Text-fig. 4A: 4), as in *Hunnegraptus copiosus*. This change in the stipes is apparently coupled with a reduction in total thecal length. A growth stage preserved in relief (Text-fig. 4F), might give a clue as to the disappearance of the sicular bitheca. It appears to have the proximal part of the bitheca, which has stopped growing. The 'aperture' is covered by periderm. Since only one specimen has been found, this interpretation is uncertain. The specimen could be pathological or deformed by compression.
5. The last primitive character, the sicular bitheca, is lost, and the 'dichograptid' development stage is reached (Text-fig. 4A: 5).

In addition to what I have observed, Williams and Stevens (1991), using isolated specimens, found that residual bithecae may be found associated with dichotomies after disappearance of bithecae from the rest of the stipes.

Phylogeny. The phylogeny of the fauna is difficult to trace, mainly because of the rarity of well-preserved graptolites of Late Tremadoc age. What is evident is that the *Paradelograptus* group flourished in Early Hunneberg time, with at least six species present in Scandinavia. The genus belongs in the family Sinograptidae (see further discussion with systematic descriptions) which, judging from proximal and thecal characters, derives its origin from *Adelograptus tenellus*, and thus not *via* an unspecified dichograptid, as suggested by Fortey and Cooper (1986, text-fig. 11). The Sinograptidae constitutes one of the independent lineages with bithecal reduction. Another is the *Clonograptus s.s.* lineage. The earliest representatives of the lineage known from relief material



TEXT-FIG. 4. The observed steps in the evolution from a regularly bithecate anisograptid to a dichograptinid. A, 1–5 shows a hypothetical development plan, involving the observed combinations of primitive and advanced characters. B, diagrammatic sketch of the budding principle of *Kiaerograptus*; dotted lines show thecal outlines on the unexposed side. C, PMO 72.834, Upper Tremadoc Ceratopyge Shale, Slemmestad, an unidentified stipe fragment showing irregular triad budding with four consecutive bithecae on the same side of the stipe; × 15, drawn from latex cast under vertical light. D, the same slab, a distal part of a large *Kiaerograptus kiaeri* specimen with three consecutive bithecae on the unexposed side of the stipe; × 15, drawn from latex cast under vertical light. E, diagrammatic sketch of a stipe with plaited thecal structure, based on a specimen of *Clonograptus* (*C.*) aff.

(Lindholm and Maletz 1989) have a sicular bitheca and plaited thecal structure (*C.* aff. *multiplex*) or a sicular bitheca and normal dichograptid stipes (*C. rigidus*). Lindholm and Maletz (1989) restricted *Clonograptus s.s.* to species without bithecae along the stipes. *Hunnegraptus* is a probable descendant of an early *Clonograptus* species or of one of its ancestors. A certain variation in first-order stipe length is known in *Clonograptus*, and the length was accentuated in *Hunnegraptus*. It is possible that one group of didymograptids (*D. undulatus*, *D. protobalticus–balticus*, *D. geometricus* etc.) derives its origin from *Hunnegraptus*, through suppression of higher-order dichotomies. Likewise, a number of horizontal and reclined tetragraptids (and *Dichograptus* species?) may derive their origin from a species of *Clonograptus s.s.* related to *C. magnificus–multiplex*. Broad stipe fragments with thecae of reclined tetragraptid type (long, somewhat curved thecae, with high inclination and high thecal overlap) are sometimes met with in the Lower Hunneberg fauna.

Other taxa are more problematic. For instance, did *Kiaerograptus* give rise to another group of didymograptids (another separate lineage with bithecal reduction) and/or the earliest isograptids (see p. 320)? What is the origin of the early 'corymbograptids' found in Scandinavia, Britain and Spain – probably the very earliest didymograptids – and the 3- and 5-stiped forms?

SYSTEMATIC PALAEONTOLOGY

Repositories of specimens. Abbreviations used are as follows: GPI, Institute of Geology and Palaeontology, Göttingen, Germany; GSC, Geological Survey of Canada, Ottawa, Canada; LO and LR, Department of Historical Geology and Palaeontology, Lund, Sweden; PMO, Palaeontological Museum, Oslo, Norway; PU, Palaeontological Institute, Uppsala, Sweden; RM, National Museum of Natural History, Stockholm, Sweden; SGU, Geological Survey of Sweden, Uppsala, Sweden; TUB, Technical University, Berlin, Germany.

Order GRAPTOLOIDEA Lapworth, 1875

Diagnosis (from Fortey and Cooper 1986). Graptolites in which the nema is retained in the adult stage.

Incerti subordinis

Family ANISOGRAPTIDAE Bulman, 1950

Diagnosis (from Fortey and Cooper 1986). Paraphyletic group, sicula retains nema in adult stage, bithecae present, rhabdosome more or less bilaterally symmetrical, and quadriradiate, triradiate or biradiate.

Remarks. The Anisograptidae is a very heterogenous group, with many of its biradiate taxa closely similar to various taxa within the Dichograptina, the only difference being the presence of bithecae along the stipes in anisograptids. In my opinion, to obtain a phylogenetically based classification, the inclusion of taxa with bithecae along the stipes will eventually have to be accepted in the Dichograptina, thus necessitating a redefinition of that group. What would be left in the Anisograptidae, in that case, would be its tri- and quadriradiate taxa, which are probably rather closely genetically related, since they appear in a relatively short interval of time just after the origin of planktonic forms. Additionally included would be those biradiate taxa that cannot be linked with a dichograptinid form. For practical purposes, this change would make classification (above the genus level) easier, since most forms are not well enough preserved to reveal bithecae.

Genus KIAEROGRAPTUS Spjeldnaes, 1963

Type species. Kiaerograptus kiaeri (Monsen, 1925).

Diagnosis (based on Spjeldnaes 1963; Rushton 1981; and author's observations). Rhabdosome biradiate, composed of two reclined to declined stipes, one of which may be aborted after the first theca; one stipe may branch near, or at some distance from, the sicula. In some rare cases, an extra proximal theca may represent an aborted third stipe. Autothecae are of dichograptid type but may have isolated distal parts. Bithecae present at sicula and along stipes. Triad budding not always regular.

Kiaerograptus supremus sp. nov.

Text-fig. 5

v 1965*a* *Kiaerograptus kiaeri* (Monsen); Erdtmann, pp. 106–107, pl. 2, figs 1 and 2; pl. 3, fig. 4.

Name. Latin *supremus*, uppermost, indicating its position as the last of the fully bithecate species in the Krapperup core.

Material. 46 specimens, of which 44 come from the 151·96–144·57 m level of the Krapperup core and 2 from the Toyen section, Oslo (both found on PMO 73.652; illustrated by Erdtmann 1965*a*). Holotype LO 5970T (Text-fig. 5A), paratype LO 5971t.

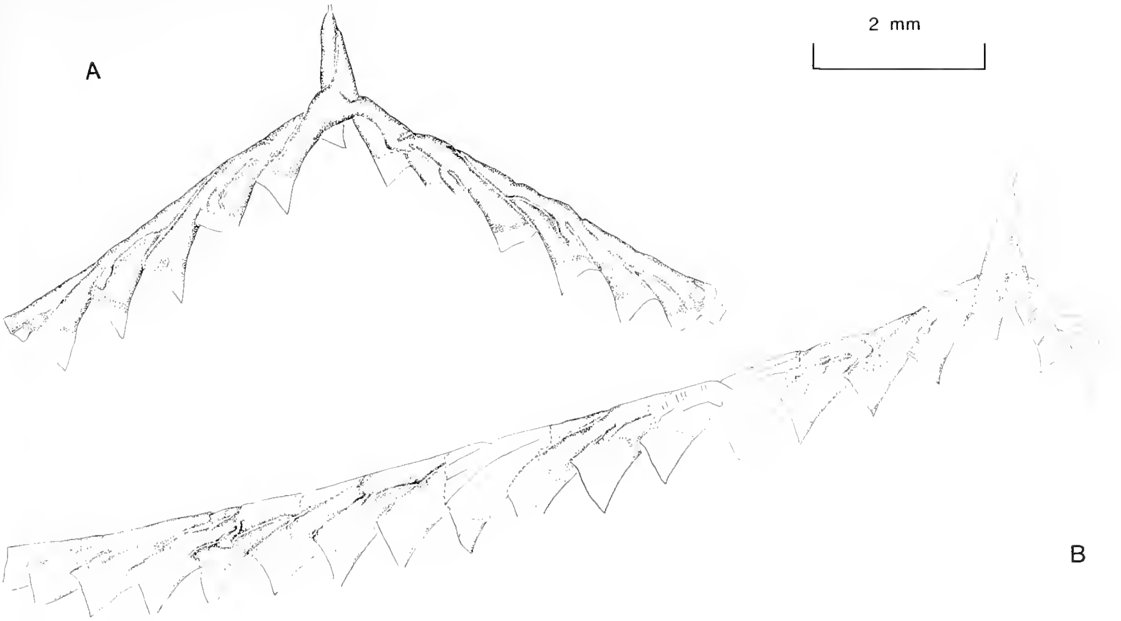
Associated species. ?*Trograptus* sp., *P. onubensis*, *A. murrayi*.

Stratigraphic range. *K. supremus* and *A. murrayi* Zones.

Diagnosis. Rhabdosome composed of two undivided declined stipes. Proximal development comparable to isograptid type. Bithecae present throughout stipes but sometimes not regularly alternating. Length of sicula 1·7–2·0 mm, stipe width 0·8–1·1 mm, 12–13 thecae in 10 mm, divergence of stipes 115–140°.

Description. The species is a typical anisograptid, with bithecae developed at most or all available nodes (with possible reductions in the stratigraphically youngest specimens – no pyritized specimens are available above 147·66 m). The proximal development type resembles the isograptid development, i.e. th 1^2 is dicalycal. As seen in Text-figure 5A, though, theca 2^2 emerges from the sicula-facing side of th 1^2, indicating that the triad (alternate) budding mechanism operates already in this position. Both sinistral and dextral forms are found (compare Text-fig. 5A with 5B). A sclerotized stolon system has not been observed: a relief specimen (now unfortunately lost) from the Krapperup core, filled with clear calcite, appeared 'empty' inside. The sicula is tube-like, 1·7–2·0 mm long and 0·3–0·45 mm wide at the aperture, depending on the degree of compression. The first bud emerges approximately 0·25 mm from the apex of the sicula. The stipes show typical triad budding, i.e. the autothecae are seen to emerge alternately from opposite sides of the stipe. The first bitheca of each stipe (as well as the sicular bitheca) seems to occur on the obverse side. Thecal length, including stolothecae, can be estimated at 2 mm. Thecal width at the aperture is 0·5 mm, sometimes slightly more in flattened specimens. The free ventral part of the thecae is somewhat curved, especially if the proximal part of the theca is more completely pyritized than the distal part (see Text-fig. 5A). The inclination of the distal parts of thecae varies from 30° to 45° depending on the degree of compression. There are 12–13 thecae in 10 mm. The thecal overlap is difficult to estimate due to the triad budding: the thecae do not bud dorsally, but laterally. In regular triad budding, the budding point of every second theca is on the unexposed side of the specimen. Such a theca will be seen only as a wedge between the preceding and the following theca (see Text-figs 4 and 5). The bithecae are about 0·4 mm long and 0·1–0·15 mm wide. They do not reach the aperture of the previous autotheca. Text-figure 5B shows a stipe with irregular triad budding: the bithecae associated with th 2^2 and 4^2 are on the obverse side, whereas that associated with th 6^2 is on the reverse side. The profile stipe width is 0·8–0·9 mm in relief specimens, and 0·9–1·1 mm in flattened ones. The stipe divergence angle is 115–140°.

Remarks. Within the studied area, the species was found only in the Krapperup core and the Tøyen section in Oslo (Erdtmann 1965*a*). From the latter area only two specimens from a shale band at the very top of the Ceratopyge Limestone unit were found. This limestone is considered as the top of the Tremadoc in Scandinavia. Most or all of it is younger than the youngest Tremadoc beds present in the type area. Because the Krapperup core lacks the limestone, it is a little difficult to correlate the two occurrences of the species. On circumstantial evidence (Fågelsång core), the Krapperup specimens are somewhat younger.



TEXT-FIG. 5. *Kiaerograptus supremus* sp. nov. from the Krapperup core. A, holotype, LO 5970T, a dextral specimen in full relief, 151·46–151·50 m. B, LO 5971t, a sinistral specimen in low relief, with irregular triad budding, 150·13–150·17 m. Both specimens drawn under vertical light.

The specimens found in the Krapperup core are mostly rather small, the longest stipe seen consisting of 16 thecae (Text-fig. 5B), whereas an average stipe consists of only 3–6 thecae. On the whole, the beds with *K. supremus* are fairly poor in graptolites, at least those well enough preserved for identification. *A. murrayi* appears in the higher part of the range of *K. supremus*.

K. supremus seems most closely related to *K. klotschichini* (Obut, 1961). This species was referred to *Didymograptus*, but the original illustration (Obut 1961, pl. 1, fig. 7, 7*a*) shows indications of triad budding along the stipes. The measurements of that species are close to those of *K. supremus*, except for a shorter sicula (but the illustration gives the impression of a longer sicula than mentioned in the description) and a slightly narrower final stipe width. *K. klotschichini* was found in clay shales in the southern part of the Ural Mountains. Apparently it was not associated with any other species and its precise age is unknown. *?Didymograptus* sp. Bulman, 1954, is probably the oldest *Kiaerograptus* species so far known, found at a rather low level of the Dictyonema Shale in the Oslo region; it has an outline fairly close to that of *K. supremus*. It differs mainly in having a longer sicula, a slightly narrower final width, and stipes that distally become nearly horizontal. Bulman (1954, p. 36) noted that there was no trace of bithecae or stolothecae, but the material is totally flattened, thus making it impossible to see such details. Both *K. klotschichini* and *?Didymograptus* sp. are known only from a few specimens, so it can be supposed that only a part of the full range of variation has been revealed. Two other species, *K. kiaeri* (Monsen, 1925) and *K. quasimodo* Rushton, 1981, show a great inherent variation. I have studied the material of *K. kiaeri*, 470 specimens, that formed the basis of the publication by Monsen (1925), and among these specimens the variation in, for example, stipe attitude, number of thecae in 10 mm, and the number of thecae with isolated distal parts is such that the end members of the variation would hardly have been recognized as belonging to the same species, were it not for all the intermediate specimens. The excellently preserved material of *K. kiaeri* described by Spjeldnaes (1963) shows, in addition to this variation, at least three successive bithecae on the same side of the stipe (see Text-fig. 4D) – a type of irregularity found also in *K. supremus*. *K. quasimodo* resembles *K. kiaeri* in the variation of, for example, stipe attitude and distal isolation of thecae, but also has a variable number of stipes (which is comparatively rare in *K. kiaeri* – less than 2%): sometimes stipes are 'aborted' after their first theca (see Rushton 1981, figs 2 and 3). *K. quasimodo* also has occasional second-order branching close to the sicula, giving three-stiped specimens. Compared with these two species, *K. supremus* has differently shaped bithecae, a more constant and lower stipe divergence angle, more rigid stipes, and apparently no thecae with isolated distal parts. The stipes also diverge from the sicula closer to its aperture. I interpret the latter three characters as more advanced, probably indicating that *K. supremus* comes from a higher stratigraphical level.

Genus ARANEOGRAPTUS Erdtmann and VandenBerg, 1985

Type species. Dictyonema macgillivrayi nom. nov. T. S. Hall, 1897 (= *Dictyonema grande* T. S. Hall, 1891; *non D. grandis* Nicholson, 1873).

Diagnosis (taken from Erdtmann and VandenBerg 1985). 'Rhabdosome siculate, biradial, produced by dichotomous division (similar to *Clonograptus*), generally at steadily increasing intervals, to eighth or ninth order [or possibly more] (usually fourth to sixth); adjacent branches connected by more or less regularly spaced dissepiments; autothecae in proximal portions denticulate with concave ventral margins and of moderate inclination; bithecae not observed. Juvenile specimens, up to the third-order dichotomy, cannot be assigned to a particular species, because of their identical morphology and structural development.'

Remarks. The absence of bithecae in the type species cannot be considered proven on the basis of the Australian material used by Erdtmann and VandenBerg, since this material is completely flattened and cannot possibly reveal such characters. For this reason I leave *Araneograptus* with the Anisograptidae. Also the biradiality of the rhabdosome is not proven beyond doubt. All the illustrated details of proximal ends (Erdtmann and VandenBerg 1985, fig. 6A–C) show an asymmetry which could be interpreted, instead, as three primary stipes. If this is the case, the genus is a junior synonym of *Rhabdinopora* Eichwald.

Araneograptus murrayi (J. Hall, 1865)

Text-figs 6, 7, ?18C

	1865	*Dictyonema Murrayi* J. Hall, pp. 138–139, pl. 20, figs 6 and 7 [photographs seen].
	1865	*Dictyonema quadrangularis* J. Hall, p. 138, pl. 20, fig. 5.
	1873	*Dictyonema grandis* Nicholson, pp. 134–136, fig. 1.
v	1937	*Dictyonema* cf. *murrayi* J. Hall; Monsen, pp. 89–92, pl. 11, fig. 2.
	1982	*Dictyonema murrayi* J. Hall; Mu *et al.*, p. 295, pl. 73, fig. 1.
	1982	*Dictyonema quadrangulare* J. Hall; Mu *et al.*, p. 295, pl. 73, figs 2–4.
	1982	*Dictyonema maximum* Xu sp. nov.; Mu *et al.*, pp. 295–296, text-fig. 101, pl. 73, figs 5–7.
	1982	*Dictyonema ziyangense* Xu sp. nov.; Mu *et al.*, p. 296, pl. 74, fig. 3.
	1985	*Dictyonema pulchellum* T. S. Hall; Rushton, p. 332, figs 1 and 2.
	1985	*Dictyonema* sp. Rushton, p. 332, figs 3 and 4.
	1987	*Araneograptus murrayi* (J. Hall); Gutiérrez Marco and Aceñolaza, pp. 325–330, pl. 1.
v	1988	'*Dictyonema*' cf. *yaconense* Turner; Molyneux and Rushton, pp. 65–66, fig. 8.

Lectotype. GSC 962*a*, J. Hall's (1865) pl. 20, fig. 7; Text-fig. 6 herein; designated lectotype by Gutiérrez Marco and Aceñolaza (1987).

Material. From the Krapperup core (148.22–109.86 m), *c.* 30 surfaces (each 30 cm²) with 1– > 5 specimens of different sizes, ranging from juveniles to fragments of giants. The species is most common in the lower part of its range, up to 136·69 mm. At 141 m the species is very common, forming layers each a couple of millimetres thick.

The species is absent at Mt Hunneberg, and only a few specimens have been found in the Oslo region, all except one slab from the Slemmestad area: PMO 58.967 from the *T. phyllograptoides* Zone (more probably lower) at Galgeberg (east-central Oslo), a large specimen figured by Monsen (1937), associated with a juvenile; PMO 137 from Gjeitungholmen, Slemmestad, allegedly from the upper Tremadoc Ceratopyge Shale; PMO 108.568, 108.569, 108.572 – together containing 6 specimens (of which 3 are juveniles) from 0·5–1·0 m above the Ceratopyge Limestone at Slemmestad crossroads; PMO 112.967 + 112.969, PMO 112.969 + 112.966, two relatively large specimens from Prestengveien, Slemmestad; and PMO 120.751, three specimens from 21·70 m at the new standard section (= 4·1 m above the Ceratopyge Limestone), central Slemmestad.

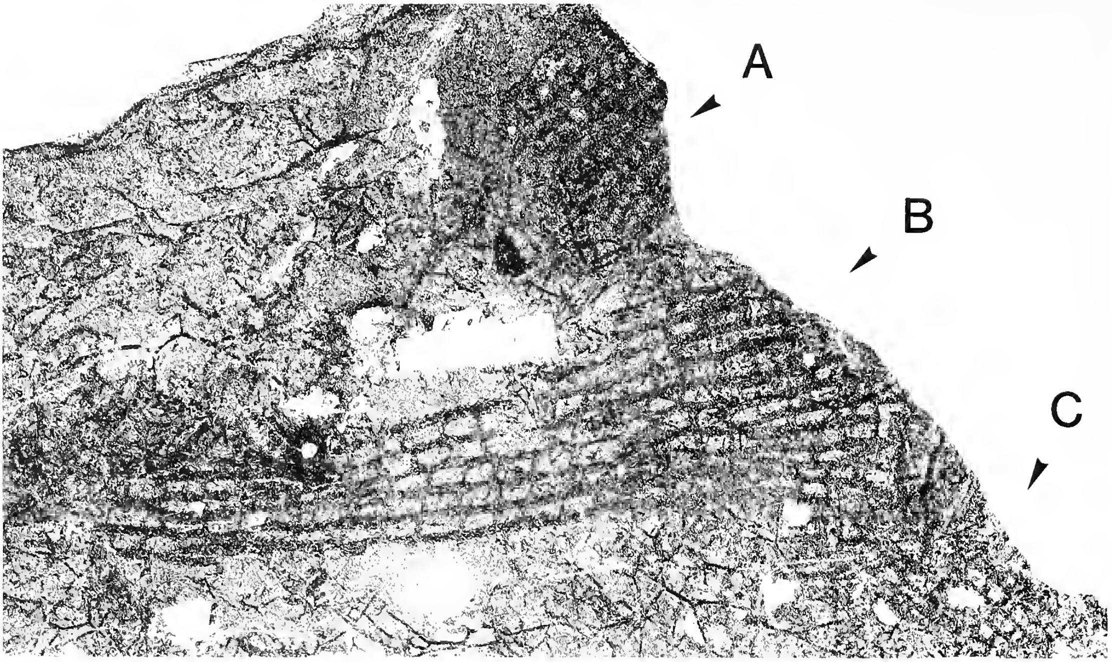
Associated species. K. supremus, H. copiosus, T. krapperupensis, horizontal tetragraptids ('quadribrachiatus'-type), three-stiped extensiform tetragraptids, *Didymograptus* sp. 1, *P. antiquus, P. elongatus, P. tenuis.*

Stratigraphic range. A. murrayi to *T. phyllograptoides* Zones, possibly also lower and higher. Maximum abundance in the *A. murrayi* Zone.

Diagnosis (based on the Scandinavian material and Gutiérrez Marco and Aceñolaza (1987)). Rhabdosome conical, mostly subtending an angle of 60–75° when flattened, angle decreasing distally in big specimens. Meshwork normally has 3–4 stipes in 10 mm, and 2–3 dissepiments in 10 mm, but the total variation ranges well outside these limits. The shape of the meshes is variable, from rectangular to oval. The lateral stipe width is over 1 mm, the thickness of the dissepiments is variable. The maximum length of the rhabdosome is unknown, but at least 30 cm.

Description. Not much is known about the details of proximal growth pattern of the species. A few immature specimens have been found at different levels in the Krapperup core. A couple of these could possibly support a biradiate origin of the rhabdosome, while others seem asymmetrical enough to indicate a triradiate origin. The sicula is 1·8–1·9 mm long where seen in full but presumably somewhat longer, perhaps up to 2·5 mm, in some more mature specimens. A very short nema of normal thickness is seen in a couple of the immature specimens. No specimen is well enough preserved to show beyond doubt a biradiate origin or any details of proximal development. At two levels (those of Text-figs 17 and 18), pyritized immature specimens of various species occur. Some of these are pendent and may belong to *A. murrayi* but, due to the lack of dissepiments, this cannot be proved unequivocally. All pendent forms seen in obverse view have a sicular bitheca. One of the specimens seen in reverse view (Text-fig. 18C), shows a dicalycal theca 1^2 and a two-stiped origin. It apparently lacks plaited thecal structure. In some of the slightly larger specimens (Text-fig. 7F, H) the sicula, and sometimes also more of the proximal region, is covered with cortical tissue, extending on to the nema, which is then up to more than 1 mm thick. A couple of thecae are seen in partial profile view in one of the immature specimens, giving an estimate of 11·5 thecae in 10 mm. The thecae seem to be straight tubes of normal dichograptid appearance. On the other hand, a Moroccan specimen (Text-fig. 7B) shows a few thecae in relief which are very denticulate, the distal part of the ventral side being almost at right angles to the dorsal margin of the stipe. This high angle could, however, be due to distortion. The thecae number about 12·5 in 10 mm in this specimen. The difference in thecal shape between the two specimens can be explained in different ways: either the thecal shape changes along the rhabdosome, or the slightly oblique position of the thecae in the Scandinavian specimens obscures their true shape. Another possibility is, of course, that there is more than one species which cannot be distinguished on the basis of cone shape and mesh pattern alone. Ruedemann (1947, p. 171) commented on the thecae thus: 'Thecae numbering 9–10 in 10 mm; apparently with acute extensions of apertural margins.' Rushton (1985, fig. 2*c*) showed elongate thecae with high overlap and high distal inclination.

Normally, only the dorsal side of the stipes is seen, since this is the outward-facing side of the cone and also represents the surface most easily exposed by splitting. The lateral stipe width is mostly 1·2–1·5 mm in flattened specimens. Specimens with some relief often have thinner stipes, down to 1·0 mm. The stipe width of immature specimens is sometimes as low as 0·6–0·7 mm. The dissepiments are rather regularly spaced within a specimen (closer in the proximal part, though), but the number of dissepiments per length unit varies markedly from one specimen to another, from about 4 in 10 mm down to 1·5. The average density is about 2–3 dissepiments in 10 mm. Also the stipe density varies between specimens. This variation is due to the frequency of dichotomies

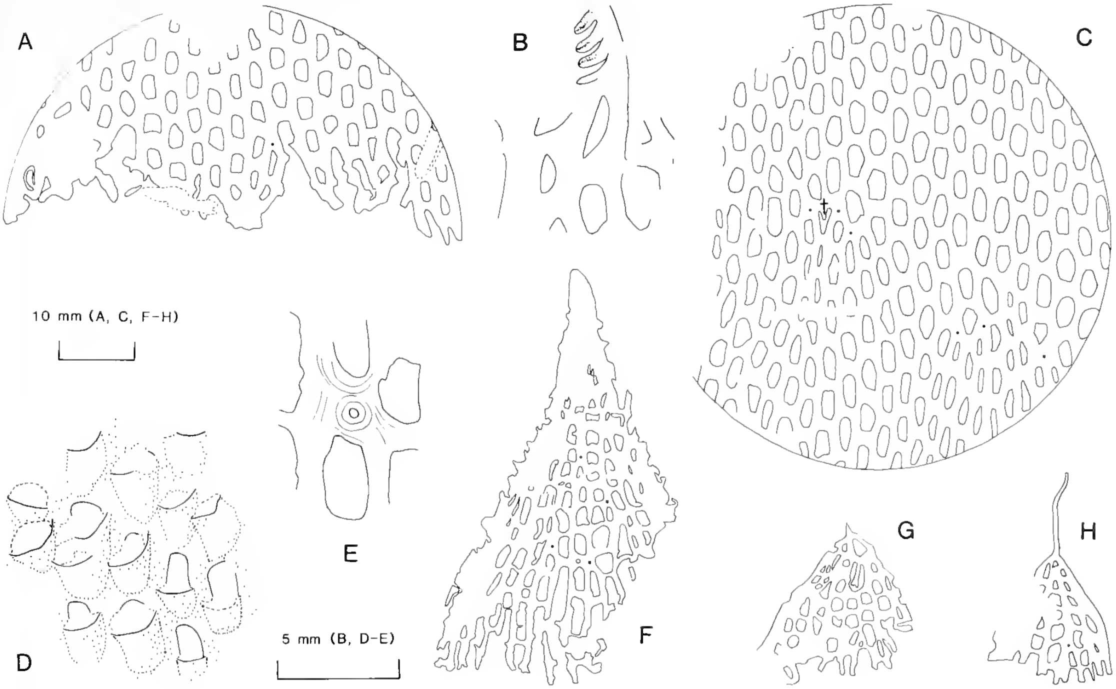


TEXT-FIG. 6. GSC 962a, lectotype slab of *A. murrayi* (J. Hall) containing three specimens, x 1. A, specimen of *quadrangularis* type with short meshes and relatively broad dissepiments. B, lectotype. C, specimen with short meshes and relatively thin dissepiments. The specimens are associated with numerous rhabdosomes of *Clonograptus rigidus*.

(see Text-fig. 7C) and the angle of the cone. There are normally about 3·5–4 stipes in 10 mm, but the total variation ranges from 3 to 5. The variation in stipe and dissepiment density gives a marked variation in size and shape of the meshes. Another factor influencing this is the thickness and shape of the dissepiments. The meshes can thus be square, rectangular, nearly circular, or oval. The thickness of the dissepiments varies from considerably thicker to noticeably thinner than the stipes, but in most specimens they are of about the same thickness as the stipes. The dissepiments are sometimes uniformly thick, in others thinner in their middle part. Secondary cortical additions to the stipes and dissepiments can, under special circumstances, almost fill out the meshes (Text-fig. 7E). The formation of dissepiments seems to have been very regular, these being inserted in every second or third position at the same time (or rather, the same distance from the sicula), so that the meshes form diagonal rows across the specimen (see Text-fig. 7A, C). This pattern is disturbed where dichotomies occur. These are relatively frequent in proximal parts (see Text-fig. 7F) but rare in the distal part of large specimens. Text-figure 7C shows two zones of stipe division, both apparently induced by irregularities in the mesh pattern. The left zone compensates for the loss of a stipe († in the figure), the right-hand one seems to compensate for a deflection to the right of one stipe, as seen by the very small mesh to the right of this stipe slightly more proximally than the point of dichotomy (this interpretation seems more probable than that a stipe division was planned for). In both cases the dichotomies compensating a disturbance are paired, followed by an additional dichotomy slightly later. Paired dichotomies were illustrated also by Rushton (1985, fig. 4).

A couple of relief specimens (see Text-fig. 7D) have what appears to be later additions attached on the outside of the rhabdosome, pouch-like 'balconies' that join the stipes on their dorsal side. They do not seem to form part of the normal dissepiments. Their function is likely to have been to direct water currents through the rhabdosome meshwork. A distal end fragment (Text-fig. 7A) shows that dissepiments are present at normal frequency to the very distal end of the stipes, i.e. they are produced as the stipe grows. Further, the distalmost dissepiments have full width, but the 2–3 last produced of them seem to be less dense. This may explain the apparent lack of strength, leading to the disruption shown in Text-figure 7A.

The angle of the cone is normally 60–75°, but in a couple of cases angles as low as 40–50° have been observed. As seen from some very large Spanish specimens, the angle of the cone decreases distally. The angles of the larger Scanian specimens were impossible to measure, since the drillcore surfaces contain only small fragments



TEXT-FIG. 7. *Araneograptus murrayi* (J. Hall). Black dots in rhabdosomes indicate the positions of stipe divisions. A, LO 5972t, Krapperup core, 137·70 m, the distal end of a large specimen; stippling indicates not fully corticized dissepiments, dashed outlines represent superposed phyllocarids. B, PMO 120.752, detail of a Moroccan specimen showing thecae in some relief. C, LO 5973t, Krapperup core, 137·60 m, part of a large specimen with relatively elongate meshes and two zones of branching; † represents the termination of a stipe. D, PMO 112.966, Slemmestad, detail of a specimen with pouch-like 'balconies'. E, PMO 58.967 (= Monsen 1937, pl. 11, fig. 2), Galgeberg, Oslo, detail showing cortical overgrowth of a mesh. F, PMO 137, upper Tremadoc (?), Gjeitungholmen, Slemmestad, a specimen with the proximal part covered by cortical tissue (stippling). G, LO 5974t, Krapperup core 147·66–147·72 m, a specimen without cortical overgrowth of the proximal part, and possibly indicating a triradiate origin. H, LO 5975t, Krapperup core 140·30 m, a specimen with cortical overgrowth of sicula and nema.

of rhabdosomes. The maximum number of stipe dichotomies is unknown but, judging from the very low number of branchings on the drillcore surfaces, the rhabdosomes must have been very big, with a cone length of perhaps more than 20 cm.

Remarks. The large Scanian specimens are closely similar to the specimen figured by J. Hall (1865, pl. 20, fig. 7), except that their dissepiments are on the average somewhat thicker. Hall, according to the figured material of *Dictyonema murrayi*, allowed a certain variation in the number of dissepiments per length unit, the specimen in plate 20, figure 6 having a dissepiment spacing equal to that of *D. quadrangularis* figured on the same plate. Hall seems to have found the thickness of the dissepiments more important than their spacing. But, on the type slab GSC 962*a*, containing plate 20, figure 7 and two additional specimens (Text-fig. 6), all three shapes co-occur on one surface, indicating their probable conspecificity.

Gutiérrez Marco and Aceñolaza (1987) also synonymized *D. yaconense* from South America and *Nyssenia zemmourensis* from northern Africa, as well as some variously named European finds, with *A. murrayi*. Interestingly, they noted that the descriptions of different species fitted different parts of one rhabdosome. They hesitated to synonymize *A. pulchellus*, although they noted that in some characters the two species were partly overlapping. Their main argument was that no specimen of *A. pulchellus* of the size of the larger *A. murrayi* specimens has ever been found. Although they did not regard *D. grandis* Nicholson as a junior synonym, I suggest that it is. According to Nicholson (1873), *D. grandis* differs from *D. murrayi* by having conical form, more frequent bifurcation, and meshes wider than long. The first two differences are easily explained by Nicholson's specimen being the proximal part of a rhabdosome and Hall's specimens more distal fragments. The third difference, the shape of the meshes, can be explained by tectonic distortion, coupled with more closely-spaced dissepiments in the proximal part of the rhabdosome. Both J. Hall's and Nicholson's types derive from Lévis, Quebec.

A. murrayi has a world-wide distribution, including Europe (Scandinavia, Great Britain, Germany, France, Spain), northern Africa, eastern North America, South America (as *D. yaconense*; Argentina, Bolivia), and NW China. The species was listed, but not illustrated, from the Taimyr area of the Soviet Union by Obut and Sobolevskaya (1962). A more detailed account of the distribution is given by Gutiérrez Marco and Aceñolaza (1987). In addition, the possibly conspecific *A. pulchellus* is found in Australasia and western Canada. Both species seem to be restricted to a relatively narrow stratigraphical interval, corresponding to the Australasian stage La 2, and in some cases the basal part of La 3.

Suborder DICHOGRAPTINA Lapworth, 1873

Diagnosis (from Fortey and Cooper 1986; emended by Lindholm and Maletz 1989). Graptoloids lacking bithecae along the stipes, and without virgella.

Remarks. The diagnosis by Fortey and Cooper has been emended to incorporate in the Dichograptina the anisograptid/dichograptid intermediary forms with a sicular bitheca, but without bithecae along the stipes. Since the loss of bithecae apparently occurred in different lineages during a relatively short period of time, the Dichograptina, like the Anisograptidae, will be a paraphyletic group, no matter where the boundary between the two groups is drawn (however, see remarks on the Anisograptidae, p. 291).

Superfamily DICHOGRAPTACEA Lapworth, 1873

Diagnosis (from Fortey and Cooper 1986; slightly emended by Lindholm and Maletz 1989). Dichograptinids lacking isograptid symmetry, number of orders of dichotomy in rhabdosome not limited.

Remarks. The diagnosis by Fortey and Cooper has been emended to include forms which apparently have unlimited capacity for dichotomy, e.g. the genus *Clonograptus*.

Family DICHOGRAPTIDAE Lapworth, 1873

Diagnosis (from Fortey and Cooper 1986). Dichograptaceans lacking prothecal folds and sigmagraptine proximal end.

Genus HUNNEGRAPTUS gen. nov.

Name. From Mt Hunneberg.

Type species. *Hunnegraptus copiosus* gen. et sp. nov.

Diagnosis. Dichograptids with a didymograptid proximal part and two or more orders of stipes produced by dichotomous division; first-order stipes extensiform or declined, normally consisting of approximately 5–25 thecae. Sicula tube-like; a sicular bitheca present at least in the type species. Proximal development isograptid, sinistral and dextral forms co-occurring. Thecae straight tubes of dichograptid type, no bithecae observed along stipes. Secondary cortical thickening may be present; possible stipe regeneration in gerontic specimens.

Species included. *H. copiosus* sp. nov., *H. tjernviki* sp. nov., *H. robustus* sp. nov., and provisionally *H. novus* (Berry, 1960), *H. gulinensis* (Wang, 1981), *H. minor* (Wang, 1981), *H. sichuanensis* (Wang, 1981), *H.* sp. (Wang, 1981). Wang's taxa are probably synonyms.

Remarks. The Scandinavian specimens of the genus are here divided into three contemporaneously occurring species. However, it is possible that they all belong to one species, representing different growth stages. Unfortunately, though, the 'mature' and 'gerontic' specimens are very rare compared to the 'adolescents' and a continuous spectrum of variation cannot be proven based on the available material. Therefore the three species *H. copiosus* (abundant, and the only one of the three found as immature specimens; 'young stage'), *H. tjernviki* (less common; 'mature stage'), and *H. robustus* (rare; 'gerontic stage') are here described as separate entities. If their synonymy can be proved, the name *H. copiosus* takes precedence. Synonymy would imply that all thecae kept growing through the entire life of the colony (cf. Williams and Stevens 1988), or until the apertures were covered by cortex. The 'gerontic' rhabdosomes are too flattened to prove that such 'choking' with cortex took place, but nearly all specimens of *H. robustus* have irregularly placed thin lateral stipes, as thin as those of the other two species. These stipes are connected to the main body of the rhabdosome by the cortex, and thus cannot be superimposed stipes belonging to other specimens. They do not influence the direction or thickness of the main stipes. They appear to represent a rejuvenation of the colony, extra stipes being inserted later than the surrounding branches. This could be to compensate for zooids no longer active in that part of the rhabdosome. These stipes are probably not metacladia, and I have seen no report of comparable stipe formation in any other graptoloid.

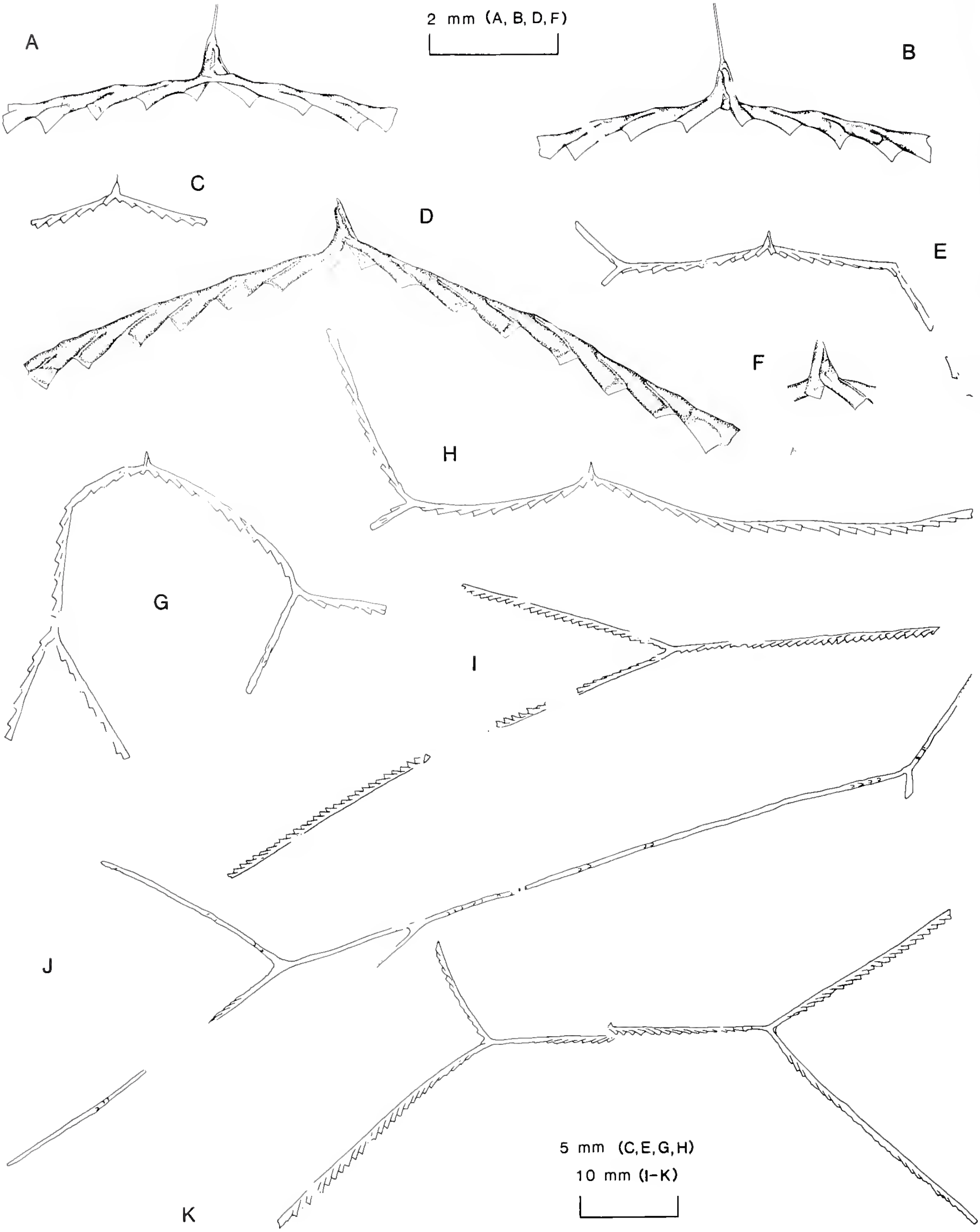
The Scandinavian occurrences are restricted to the *H. copiosus* Zone, the zone directly underlying the *Tetragraptus phyllograptoides* Zone. Provisionally included in *Hunnegraptus* is *H. novus* (Berry, 1960), which has a sicular bitheca but normally no bithecae along the stipes. This taxon is probably older than the Scandinavian occurrences, however, since it is reported to co-occur with *Anisograptus* (Berry 1960). Provisionally included are also *Kiaerograptus*? *gulinensis*, *K.*? sp., *Adelograptus minor*, and *A. sichuanensis*, all described by Wang (1981) from probable Late Xinchangian beds of Sichuan, central China. All of these are most likely conspecific, the amount of variation among them being smaller than that within the type species of *Hunnegraptus*. Multiramous species with dichograptid thecae and prolonged first-order stipes have also been described from Spain (Gutiérrez Marco 1982, 1986, pp. 290–304) and Czechoslovakia (Kraft and Mergl 1979). The material from Spain is of Early Hunneberg age, and the associated fauna contains i.a. *A. murrayi*. The age of the Czech material is uncertain. The relationship of these species to *Hunnegraptus* is not clear.

The genus is presumably most closely related to *Clonograptus*, in which first-order stipes may be prolonged, e.g. in the type species, *C. rigidus*. The sicular bitheca seen in *H. copiosus* is also found in *Clonograptus milesi*, and probably also in the type species (Lindholm and Maletz 1989). Regenerated stipes of *Hunnegraptus* type are unknown in *Clonograptus*. The latter fact has convinced me that the distinction between the two taxa should be on a generic, rather than subgeneric, level.

Hunnegraptus copiosus gen. et sp. nov.

Text-figs 8A–F and 18F, ?H, J

1987 Dichograptid sp. 1 Maletz, p. 136, text-fig. 44:9; 10, pl. 5, figs 1 and 2.
p 1987 Dichograptid sp. 2 Maletz, pp. 136–137, text-fig. 44:3?, 5–8.



TEST-FIG. 8. For legend see opposite.

Name. Latin *copiosus*, abundant, refers to the abundance of the species in all sections.

Material. 736 specimens, of which 111 come from east-central Oslo (Tøyen, 3·55–3·68 m above the Ceratopyge Limestone, and Galgeberg), 213 from various localities in the Slemmestad area, 165 from Storeklev, Mt Hunneberg, and 247 from the Krapperup core (132·73–117·00 m). Except for Krapperup, the stratigraphic range is rather limited, with specimens collected from a single horizon in a section or, as in Storeklev and the new standard section in central Slemmestad, from a relatively thin band (1·4–1·8 m and 4·6–5·6 m above the Ceratopyge Limestone, respectively). The holotype is found on PMO 58.969 from Galgeberg, central Oslo (Text-fig. 8E, F); the paratypes are LO 5976t–5979t, LO 6090t, LO 6094t, and PMO 108.599 (localities given in figure captions). The species is very common and is found on most slabs within its range, mostly as two-stiped, didymograptid-like, specimens.

Associated species. H. tjernviki, H. robustus, A. murrayi, Clonograptus s.s. sp. indet., *T. longus, T.* cf. *krapperupensis*, narrow- and broad-stiped horizontal tetragraptids ('quadribrachiatus'-type), three-stiped extensiform tetragraptids, gen. et sp. indet. 1, *Didymograptus* sp. 2, *Isograptus* sp., *P. antiquus, P. pritchardi, P. elongatus, P. tenuis, P.* cf. *rarus*.

Stratigraphic range. H. copiosus Zone.

Diagnosis. Didymograptid proximal part and one, two, or possibly more orders of stipes. First-order stipes normally declined, consisting of approx. 7–22 thecae each. Sicula mostly 1·1–1·2 mm long, sicular bitheca present. Thecae straight tubes with a thecal inclination of 15–20°. Stipe width 0·5–0·6 mm, approx. 12 thecae in 10 mm. No bithecae along stipes.

Description. The sicula is tube-shaped, 1·0–1·3 mm long, 0·25 mm wide at the aperture; and its distal part is inclined towards the stipe^2 side. The proximal part of the nema is somewhat thickened, like the cauda (Hutt 1974). A slightly curved bitheca is present on the obverse side of the sicula, budding from th 1^1 at mid-length of the sicula (Text-figs 8B, F and 18F). The aperture of the bitheca is positioned where th 1^1 bends away from the sicula. Theca 1^1 buds from the sicula approximately 0·1–0·2 mm from its apex. In early growth stages consisting of the sicula and th 1^1, the sicula and theca make a more or less symmetrical pair, with the bitheca in a central position. The proximal development type is isograptid, theca 2^1 budding from th 1^2 in its most proximal part. There are both sinistral and dextral specimens (compare Text-fig. 8A with 8D) but too few well-preserved specimens have been found for any statistical evaluation of predominance. The proximal part of the protheca is relatively narrow, resulting in a rather low thecal inclination (15–20°). A slight prothecal folding can be seen in pyritized relief specimens (Text-fig. 8A, B, D). The metathecae are simple tubes, straight or nearly so; the total thecal length is about 1·2 mm, the dorsoventral thecal width at the aperture about 0·25–0·3 mm. The thecal overlap is about 40–50%, and there are normally 11·5–13 thecae in 10 mm (total range 10·5–14). The profile stipe width is 0·5–0·6 mm, bithecae are absent along stipes, both in their proximal and distal parts. The first-order stipes consist of 7–22 thecae (observed range) and make an angle of about 120–180° (normally 130–160°) if seen in profile view. A pyritized specimen possibly belonging to the species (Text-fig. 18H) shows a first-order stipe consisting of only 3 thecae. Stipe division is dichotomous; the longest second-order stipes

TEXT-FIG. 8. A–H *Hunnegraptus copiosus* sp. nov. A, B, LO 5976t and LO 5976+, Storeklev 2·15–2·32 m, counterparts of a dextral relief specimen. C, LO 5977t, Storeklev 2·32 m, an almost flattened specimen, showing the most typical appearance of the species. D, PMO 108.599, Slemmestad, a full relief sinistral specimen; note the difference in thecal spacing between the stipes: associated specimens show no tectonic distortion. E, F, holotype, PMO 58.969, Galgeberg, east-central Oslo, a sinistral specimen (proximal part is a mould) with the fourth second-order stipe presumably primarily missing; part of one stipe is pyritized, showing absence of bithecae; F is drawn from a latex cast and shows the sicular bitheca in low relief. G, LO 5978t, 22·2 m in the standard section, Slemmestad, a dextral specimen (the sicular part is a mould), one of the bigger specimens, in a preservation showing the low degree of rigidity of the stipes. H, LO 5979t, associated with specimen shown as A and B; the specimen has highly unequal length of first-order stipes. A, B, D, F are drawn from latex casts under vertical light. I–K, *H. tjernviki* sp. nov. I, PU Vg 125, Storeklev 227–230 cm, a stipe fragment in profile view. J, LO 5980t, Grundvik, Slemmestad, the longest stipe fragment, showing four orders of stipes; the drawing is a combination of counterparts. K, holotype, PU Vg 124, Storeklev 227 cm.

seen are more than 40 mm long. A branching stipe fragment probably belonging to the species (Text-fig. 18J) shows isograptid type branching. No complete specimen shows more than two orders of stipes, but it cannot be excluded that the branching continues. In one specimen (LR 6, from Storeklev) an 'aborted' stipe division can be seen: part of a theca projects from the dorsal side of a stipe, but the stipe continues in its previous direction. Also the holotype may have lost a stipe in the same way (Text-fig. 8E): no trace of a fourth second-order stipe is seen, but in this case the stipe is bent as if branching had occurred. The majority of the specimens found are too small for branching to have occurred. These specimens look like declined didymograptids, but relief specimens in obverse view show the characteristic sicular bitheca. No marked secondary cortical thickening has been observed in this species. Specimens are often somewhat flexuous. No gerontic specimens were found, however, and the possibility of cortical thickening at a later growth stage cannot be ruled out.

Remarks. The low thecal inclination and the faint prothecal folding observed in relief specimens of *H. copiosus* might suggest a relationship with the Sigmagraptidae. However, the proximal part differs markedly from that of the type species of *Sigmagraptus* (cf. Cooper and Fortey 1982, fig. 61): the length/width ratio of the sicula is smaller, the prothecal part of theca 1^1 is shorter, th 2^1 buds off th 1^2 slightly later, so that it crosses th 1^1 instead of following its dorsal side, and also neither th 1^1 nor th 1^2 has the characteristic sharp bend seen in sigmagraptids. Except for the sicular bitheca, the proximal structure in *Hunnegraptus* is normal dichograptid. The presence of both sinistral and dextral forms must be assumed to be a primitive character (common among the Anisograptidae).

The Chinese species described by Wang (1981) are all very similar to *H. copiosus*. The illustrations show a proximal part virtually identical to that of *H. copiosus*, and sicular length and figures given for thecal characters differ insignificantly from those of that species. The only visible difference lies in the position of second-order dichotomy, which is closer to the sicula in the Chinese species. All the specimens illustrated by Wang (1981) have one or two stipe orders, like *H. copiosus*. *H. novus* (Berry, 1960) is known only as a two-stiped form. Also this taxon has a thecal shape reminiscent of *H. copiosus*.

Hunnegraptus tjernviki gen. et sp. nov.

Text-fig. 8I–K

p 1987 Dichograptid sp. 2 Maletz, pp. 136–137, fig. 44:1, 2, 4; pl. 5, fig. 3.

Name. In honour of Torsten Tjernvik, the discoverer of the Early Hunneberg graptolite fauna.

Material. 32 more or less fragmentary specimens, of which 11 are from Oslo, 10 from the Slemmestad area, 9 from Storeklev, and 2 from Krapperup. The range coincides with that of *H. copiosus*. Holotype PU Vg 124 (Text-fig. 8K) and paratype PU Vg 125 from Storeklev; paratype LO 5980t from Grundvik, Slemmestad.

Associated species. H. copiosus, T. longus, P. antiquus.

Stratigraphic range. H. copiosus Zone.

Diagnosis. Didymograptid proximal part and up to four or possibly more orders of stipes. First-order stipes horizontal or slightly declined, consisting of several thecae. Sicula approximately 1·5 mm long, sicular bitheca suspected. Thecae straight tubes with an inclination of about 30°. Stipe width 0·8–1·2 mm, about 11·5 thecae in 10 mm. No bithecae along stipes.

Description. The species is known from fewer specimens, and also in less detail, than *H. copiosus*. Most specimens consist of stipe fragments only. The sicula is about 1·5 mm long; no specimen is well enough preserved to reveal a possible sicular bitheca or the proximal development. The thecae are simple straight tubes, approximately 1·4–1·7 mm long and 0·4–0·5 mm wide at the aperture. The thecal inclination is about 30° in full profile view, less in obliquely preserved specimens. Profile stipe width is 0·8–1·0 mm in proximal parts, 0·9–1·2 mm in more distal parts; lateral stipe width (dorsoventral view) is about 0·5–0·6 mm. There are 10·5–12 thecae in 10 mm, and the thecal overlap is about 50%. Bithecae are not present along the stipes. The observed length of first-order stipes falls within the range of variation seen in *H. copiosus*; the branching is dichotomous. The first-order stipes diverge at ?150–180°. A stipe fragment from Grundvik, Slemmestad (Text-fig. 8J) shows four orders of stipes, the most proximal stipe seen being of second or higher order, judging from the angles of dichotomy. Cortical thickening of stipes is variable, but mostly not readily observed.

Remarks. The species differs from *H. copiosus*, and the species described by Wang (1981), primarily in having broader and somewhat more rigid stipes. The more rigid appearance might be explained in part by longer thecae and higher thecal overlap and in part by slight cortical thickening. In contrast to *H. copiosus*, no immature specimens of *H. tjernviki* have been observed.

Hunnegraptus robustus gen. et sp. nov.

Text-fig. 9

? 1987 Dichograptid sp. 3 Maletz, p. 138, pl. 5, fig. 4.

Name. Denoting the robust character of the species, as compared to *H. copiosus* and *H. tjernviki*.

Material. Six specimens, all illustrated in Text-figure 9. Holotype LO 5981T, from 2·60 m at Storeklev, Mt Hunneberg. Paratypes PU Vg 126, LO 5982t, LO 5983t, from the graptolite-rich band 2·15–2·32 m at Storeklev; LO 5985t, Storeklev, 2·60 m; LO 5984t from Grundvik.

Associated species. H. copiosus.

Stratigraphic range. H. copiosus Zone.

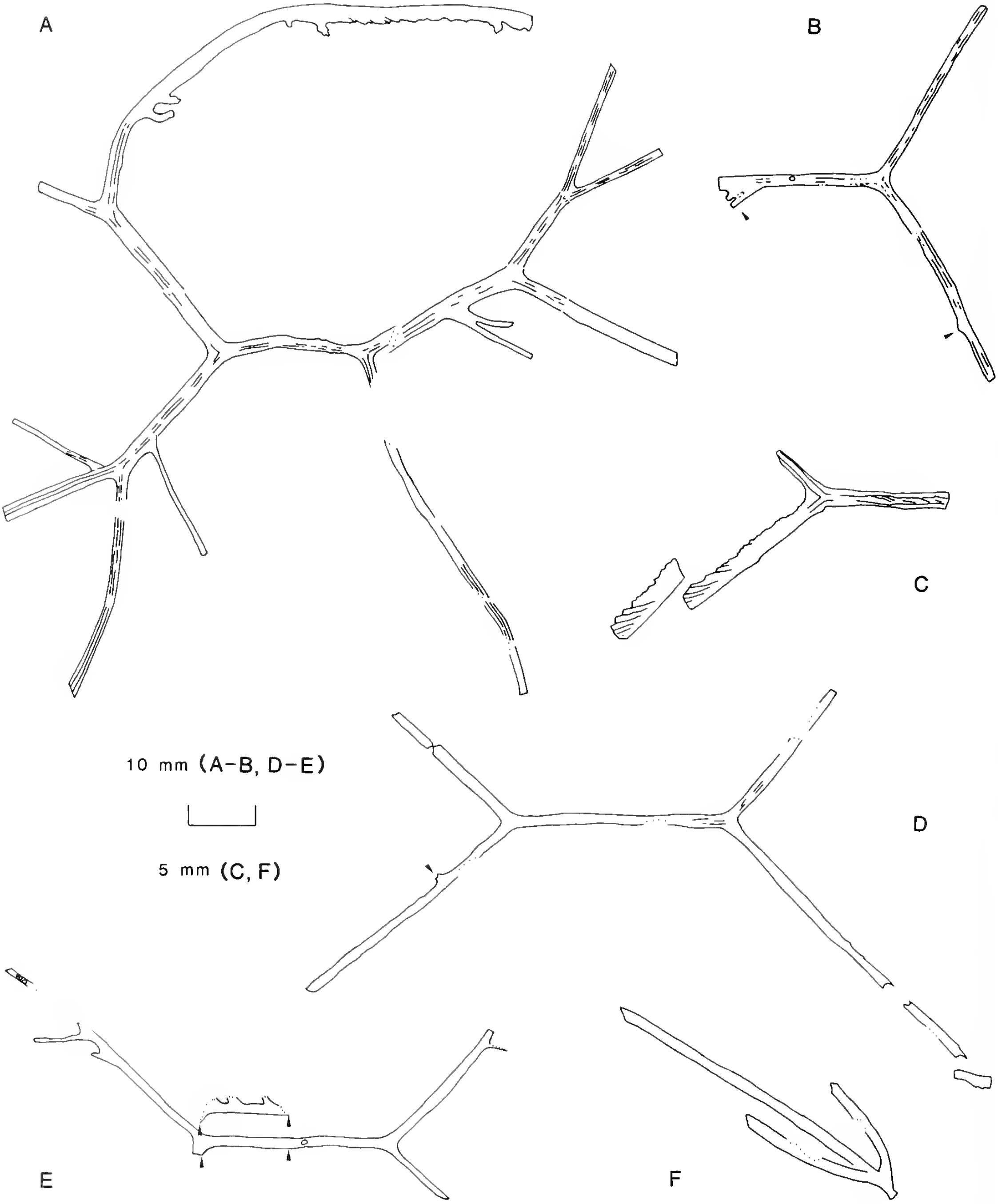
Diagnosis. Didymograptid proximal part and up to four or more orders of stipes. First-order stipes consist of several thecae. Profile stipe width 1·8–2·5 mm; lateral stipe width 1·0–2·5 mm, depending on cortical cover. Dichotomous and irregular lateral branching. Lateral stipes usually narrower than the rest of the rhabdosome.

Description. The sicula and proximal development are unknown, since only distal parts are seen in profile view. The observed combined length of first-order stipes is 24–33 mm; the observed range of second-order stipes is from 24 to more than 50 mm. The thecae are long straight tubes, their length *c.* 3 mm, width 0·4 mm, and overlap about 75%. There are about 12 thecae in 10 mm. The profile stipe width is 1·8–2·5 mm (Text-fig. 9C). The lateral stipe width varies considerably, depending on the amount of secondary cortex cover: normally 1·5–2·5 mm, but in some cases as thin as 1·0 mm. Secondary cortical cover is less marked in a distal direction, but this is in no way regular (see Text-fig. 9A). Thin (0·7–1·0 mm wide) lateral stipes occur irregularly in five of the six specimens (see Text-fig. 9A–B, D–F). These stipes are connected to the rest of the rhabdosome by the cortical thickening, and thus cannot represent superimposed fragments of other specimens. As discussed for the genus, I consider these stipes to have been formed secondarily and thus ignore them when counting the stipe order: the maximum found is four stipe orders, in the holotype. Text-figure 9E shows a specimen and its counterpart, with three broken lateral stipes seen on the counterpart only (after some preparation), indicating that they did not grow in the plane represented by the four main stipes. The lateral stipes shown in Text-figure 9F seem to have been originally directed slightly upwards, and later bent down to the bedding plane by compaction.

Remarks. The species differs from the other two described *Hunnegraptus* species, and the species of Wang (1981), in its longer thecae, more robust stipes and thick cortex cover, as well as the occasional lateral stipes. No immature specimens have been identified. The lateral stipes appear to have been formed later than the surrounding parts of the rhabdosome (see the remarks on the genus).

Genus CLONOGRAPTUS Nicholson, 1873

Type species. Graptolithus rigidus J. Hall, 1858.



TEXT-FIG. 9. *Hunnegraptus robustus* sp. nov. A, holotype, LO 5981T, Storeklev 2·60 m, showing numerous thin lateral stipes, possibly a sign of regeneration; the drawing is a combination of counterparts. B, LO 5982t, Storeklev 2·32 m, arrows point to lateral stipes; note the two closely arranged stipes on the first-order stipe, connected proximally by cortical tissue. C, LO 5983t, Storeklev 2·15–2·32 m, a stipe fragment showing thecae in profile view. D, PU Vg 126, Storeklev 227–230 cm, the specimen commented on by Tjernvik (1956, *Diagnosis* (from Lindholm and Maletz 1989). Dichograptid with bilateral rhabdosome produced by dichotomous division occurring at irregular intervals; second dichotomy in most species consecutive, forming a tetragraptid proximal part, but can be delayed for a couple of thecae; branches diverging proximally, while distally diverging, subparallel, or flexuous; thecal shape variable, unknown in many species assigned to the genus; central disc unknown, secondary development of cortical overgrowth in many species, particularly in proximal parts.

Remarks. The genus *Clonograptus* was treated by Lindholm and Maletz (1989). It was reinterpreted as a form genus (*Clonograptus sensu lato*) consisting of the phylogenetically based subgenus *Clonograptus* (*Clonograptus*) (= *Clonograptus sensu stricto*) and additionally a number of species not known in enough detail for inclusion in any phylogenetically based group. In the same paper *Clonograptus* was transferred to the Dichograptidae, since there are no bithecae along the stipes in the type species.

Clonograptus cf. *norvegicus* Monsen, 1937

Text-fig. 10F

cf. 1937 *Clonograptus norvegicus* Monsen, pp. 198–200, pl. 20; *non* pl. 5, fig. 22.
cf. 1987 *Clonograptus norvegicus* Monsen; Maletz, p. 58, fig. 41:1, 2.

Material. One incomplete, nearly flattened, specimen with proximal part, associated with scattered stipe fragments of the species, found on PMO 73.200 and 73.204 (counterparts), in grey shale from 0·5 m above the Ceratopyge Limestone at Bodalen, Slemmestad.

Associated species. None.

Stratigraphic range. *H. copiosus* Zone, possibly also *T. phyllograptoides* Zone.

Diagnosis (of *C. norvegicus*, based on Monsen 1937). A clonograptid, irregularly branching to at least 13 orders of stipes. Second- to fourth-order stipes progressively longer, but within 3–8 mm in length; higher orders on average 10 mm long or more. A marked cortex cover (peridermal film?) gives a lateral width of 3 mm proximally and down to less than 2 mm distally. The cortex obscures all thecal details. Possibly 8–9 thecae in 10 mm.

Description. In my specimen, no details of proximal development or thecae are visible due to the cortex cover and the horizontal orientation of the rhabdosome. The position of the sicula can be seen, and the outline of the stipes and branching points within the cortex film can be partly discerned, indicating that the primary stipes are of unequal length. There is probably one theca in one first-order stipe and 2–3 in the other. The thecal spacing is unknown, however, and if it is much less than 10 in 10 mm it could indicate that the specimen is triradiate rather than biradiate. The lateral width of the stipes excluding the cortex cover is 0·3–0·6 mm, the total lateral width varies from 1·5 to 2·0 mm in the proximal part down to less than 1 mm in distal parts. The branching pattern seems to be somewhat irregular, but in general the distances between branchings increase in a distal direction. Seven orders of stipes are seen, and the length of second- to fifth-order stipes are (assuming two primary stipes) 2–6 mm, 3–7 mm, 4–9 mm, and 6–10 mm. The specimen may not have been fully planar; it appears that at least one stipe crosses the others at a lower level in the slab. The branching angles are variable, *c*. 60–120° in proximal branchings and 45–70° in the more distal parts. Higher-order stipes sometimes curve to adopt a more parallel orientation.

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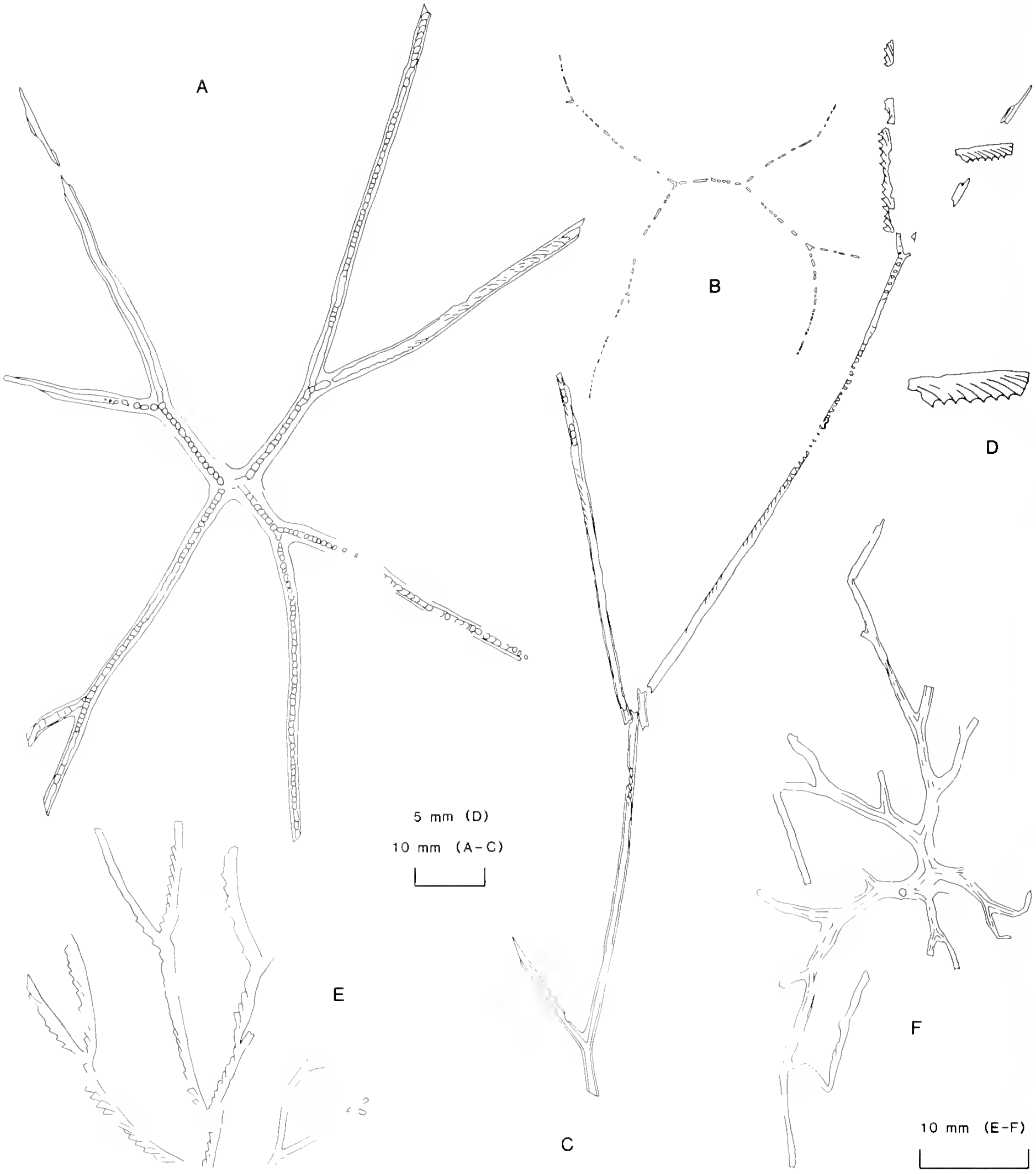
pp. 117–118); a broken lateral stipe (arrow) is seen on the lower left stipe. E, LO 5984t, Grundvik, Slemmestad, piece and mirror image of counterpart shown to illustrate lateral stipes at an angle to the plane formed by the main stipes; the lateral stipes on the upper left are connected to the main stipe by thick cortex proximally. F, LO 5985t, Storeklev 2·60 m, a stipe fragment with paired lateral stipes. Stippling indicates flexure – the lateral stipes were originally directed upwards.



TEXT-FIG. 10. A, C, D, *Clonograptus magnus* sp. nov; A, holotype PMO 108.564–108.565, Slemmestad; the drawing is a combination of counterparts; C, D, PMO 108.561–108.562, same locality as A; D is an enlargement of the obliquely positioned fragment in C, showing the thecae in profile view; C is combined from piece and counterpart. B, *Clonograptus* sp. 1, PMO 97.708, Slemmestad; drawing from latex cast. E, *Clonograptus* sp. 2, LO 5986t, Krapperup core 142·46–142·56 m. F, *Clonograptus* cf. *norvegicus*, PMO 73·200, 73·204; the drawing is a combination of counterparts.

Remarks. The fragmentary nature and lack of information on proximal development and thecal shape of the specimen makes identification very difficult. *C. norvegicus* is a rare species and the original description by Monsen (1937) was based on only one specimen with most details obscured by the cortex cover. That specimen has at least 13 orders of stipes and is more robust than the present specimen, which is unlikely to have been of that size. The robustness may be caused entirely by a thicker cortex cover, associated with its greater size. Monsen's specimen was said to be associated with '*Didymograptus minutus* var. *pygmaeus*', hence Monsen assigned it to the middle part of the Arenig. However, small pendent specimens very much resembling *D. minutus* occur also at a level slightly below the base of the *T. phyllograptoides* Zone (see Text-fig. 14C, F). Monsen's specimen comes from Grundvik, Slemmestad, one of the localities where the beds below the *T. phyllograptoides* Zone are easily accessible. Erdtmann (1965*b*, p. 496) reported having found fragments of the species at a very low level in the Toyen section. However, his specimens have since been lost and the statement cannot be verified.

Maletz (1987) reported the species from Mt Hunneberg, from the localities Tunhem and Storeklev. At the latter locality it was found at the same level as the richest finds of the *H. copiosus* fauna. Large-sized stipe fragments with thick cortex cover are present also in the *T. phyllograptoides* Zone at Mt Hunneberg (one specimen from Mossebo, SGU collections) as well as at Galgeberg, Oslo (Bergen Museum, Monsen collection 231).

The only other *Clonograptus s.l.* species of a similar outline is *C. trochograptoides* Harris and Thomas, 1939. The pattern of branching and cortex cover is identical, but stipes of a given order are somewhat shorter, giving a more compact rhabdosome. *C. trochograptoides* was said to have thecae of *Clonograptus s.s.* type, 8–9 in 10 mm.

Subgenus CLONOGRAPTUS (CLONOGRAPTUS) Nicholson, 1873

Diagnosis. As for genus, but with thecae straight or slightly curved simple tubes, overlapping one-third to two-thirds of their length; proximal development isograptid, dextral.

Remarks. A number of genera were synonymized with *Clonograptus* (*Clonograptus*) by Lindholm and Maletz (1989), most importantly *Temnograptus* Nicholson, 1876.

Clonograptus (*Clonograptus*) *magnus* sp. nov.

Text-fig. 10A, C, D

Name. Latin *magnus*, big.

Material. One specimen with proximal part preserved (holotype PMO 108.564–108.565; Text-fig. 10A) and one distal stipe fragment (paratype PMO 108.561–108.562) from 0·5–1·2 m above the Ceratopyge Limestone at Slemmestad crossroads. Additionally there are four stipe fragments from 3·42–3·60 m (+ a gap of unknown extent, probably 0·5–2 m) above the Ceratopyge Limestone at Grundvik, Slemmestad.

Associated species. *H. copiosus*, reclined *Tetragraptus* indet. (juvenile).

Stratigraphic range. *H. copiosus* Zone, possibly also *T. phyllograptoides* Zone.

Diagnosis. A very robust *Clonograptus s.s.* with a considerable cortical thickening in mature specimens. Tetragraptid proximal part, second-order stipe length approximately 10–40 mm, third and higher order generally over 40 mm. There are at least five stipe orders. 9–10 thecae in 10 mm, thecal overlap two-thirds or more, profile stipe width 1·5–2·0 mm.

Description. Details of the proximal development are unknown. In the only specimen with proximal part (Text-fig. 10A), first-order stipes consist of one theca each and second-order stipes are from 10 to 38 mm long. The specimen does not show complete third-order stipes, but the five longest fragments are 38–54 mm long.

The angle between the second-order stipes is rather high, *c.* 105°, whereas the angle between the third-order stipes is low, *c*, 45–70°. There are 9–10 thecae in 10 mm. A third-order stipe is preserved in partial profile view, giving an estimate of profile stipe width of 1·5 to 2·0 mm. As far as can be seen the thecae are rather long and narrow. All of this specimen is covered by cortex, giving a lateral stipe width of approximately 4 mm for the first-order stipes, 2·5–2·8 mm for second-order stipes, and 1·5–2·3 mm for third-order stipes.

The largest stipe fragment (Text-fig. 10 C, D) has less cortical cover than the previous specimen. The fragment has four orders of stipes, the most proximal one probably of third or higher order. The length of the two middle orders of stipes is 47 and 77 mm. There are 9·5 thecae in 10 mm. The thecae are slightly curved, with about two-thirds to three-quarters of overlap. The thecal apertures are concave. The profile stipe width is 1·8 mm and the lateral stipe width is 1·3–1·5 mm. There are no bithecae.

The remaining stipe fragments contain only one dichotomy each. They all have 9–10 thecae in 10 mm, and a profile stipe width of 1·5–2·0 mm.

Remarks. The only *Clonograptus* species of a comparable size are *C. multiplex* (Nicholson, 1868) and *C. magnificus* (Pritchard, 1892). Neither of these have the massive cortical thickening characteristic of this species. Also, its branching angles differ from those of these two species.

A stipe fragment from Taimyr, identified by Obut and Sobolevskaya (1962) as *Temnograptus* aff. *noveboracensis* Ruedemann, may be conspecific with *C. magnus.*

Form genus TETRAGRAPTUS Salter, 1863 (= TETRAGRAPTUS *s.l.*)

Tetragraptus longus sp. nov.

Text-figs 11 A–D and 12

Name. Latin *longus*, long, referring to the length of the stipes.

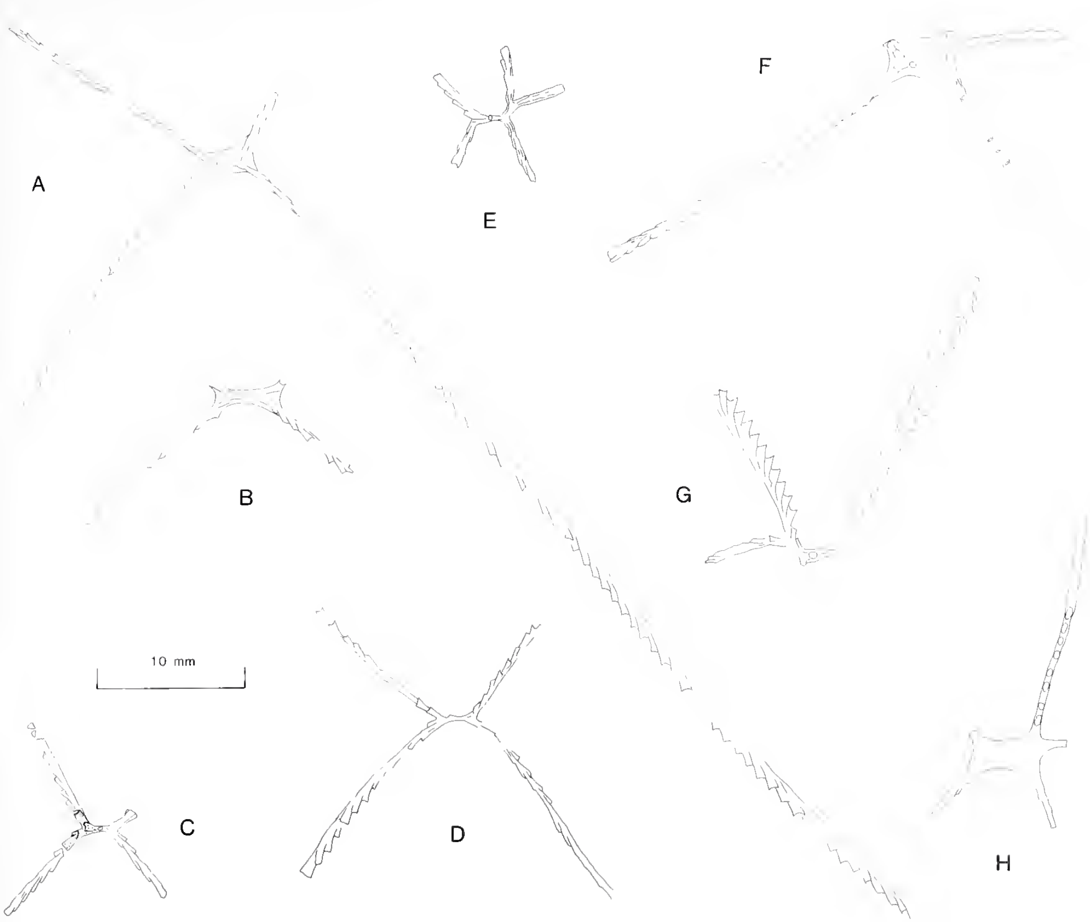
Material. 121 specimens in all, most of them more or less broken. Nearly all of them are from Galgeberg, east-central Oslo (found on PMO 58.969, 58.970); 14 specimens come from Slemmestad (PMO 97.702, 97.708 and one specimen, LR 1, in the Lund collections), and one from the Krapperup core (129·46–129·54 m). The holotype is found on PMO 58.970 (text-fig. 11A), the paratypes on PMO 58.969 and 97.708.

Associated species. H. copiosus, H. tjernviki, T. cf. *krapperupensis.*

Stratigraphic range. H. copiosus Zone.

Diagnosis. A thin-stiped (0·7–1·1 mm) horizontal tetragraptid, with small central disc in mature specimens. The divergence angle between second-order stipes is 90° or less. There are 9·5–11 thecae in 10 mm. The stipes may become extremely long.

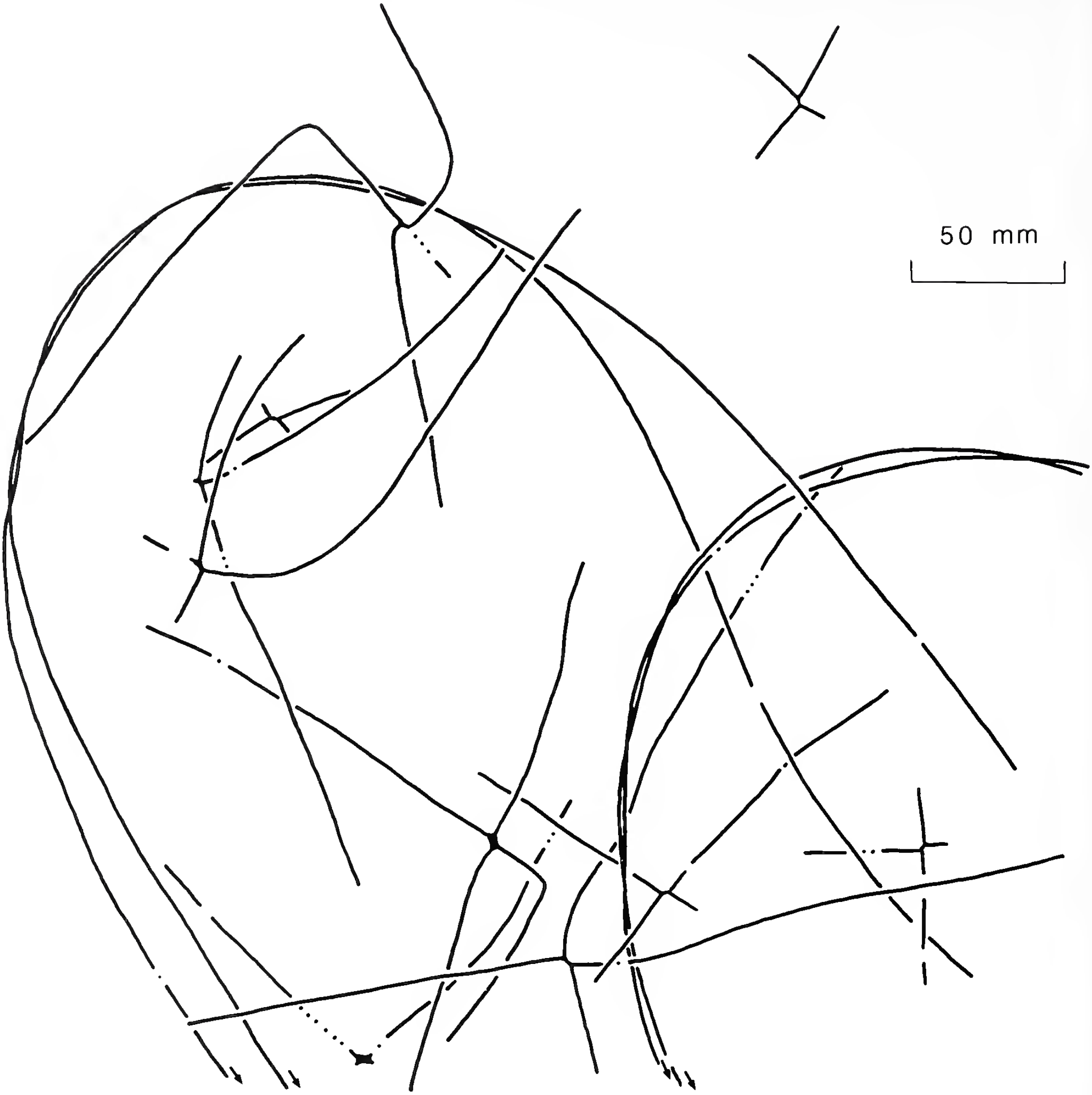
Description. The species has a normal tetragraptid proximal part (Text-fig. 11 C), i.e. the first-order stipes are composed of one theca each. All specimens are preserved horizontally, and thus do not reveal any details of proximal development or the possible presence of a sicular bitheca. Many stipes are preserved in relief and show total absence of bithecae. The stipes are 0·7–0·9 mm wide in profile view, up to 1·1 mm in very large specimens. The lateral width is about 0·4–0·5 mm, but the stipes very often show the profile view. The longest stipe fragments encountered were 710 and 680 mm respectively (Text-fig. 12; all specimens on the slab are fragmented – cf. Text-fig. 10 B – but there appears to be no tectonic distortion). They probably both belong to one specimen. The thecae are straight tubes, about three times as long as wide and with straight apertures. There are 9·5–11 thecae in 10 mm and they overlap for one half of their length or slightly less. The thecal inclination is about 20°. Mature specimens develop a small central disc (Text-fig. 11 A, B). The largest one seen is approximately 2 by 4 mm. No more than 2–3 thecae per second-order stipe are encroached upon by the disc. Cortical thickening has not been noticed along the second-order stipes, but is likely to be present to some degree, considering the relative straightness of most stipes seen in Text-figure 12. The second-order stipes normally make an angle of 80–90°, slightly more in a few specimens. The long stipe fragments in Text-figure 12 seem to have been curved by rotational movement during post-mortem descent to the sediment surface.



TEXT-FIG. 11. A–D, *Tetragraptus longus* sp. nov., Galgeberg, east-central Oslo. A, holotype, PMO 58.970, with a well-developed central disc; judging from the size of the disc, the stipes must have been very long. B–D, PMO 58.969; B, a specimen with the beginnings of a disc; C, specimen partly preserved in relief in the proximal part, showing a normal tetragraptid branching pattern; D, typical specimen, without central disc. E–H, Gen. et sp. indet. 1, all from Slemmestad. E, PMO 108.599, a complete immature specimen. F, PMO 108.566, a specimen showing the proximal branching pattern inside the central disc. G, PMO 108.567, a specimen with thecae in profile view and an immature central disc. H, PMO 108.599, proximal fragment of a presumably large specimen with a well-developed central disc.

Remarks. Thin horizontal tetragraptids are most commonly lumped together under the name *T. quadribrachiatus*. As was shown by Williams and Stevens (1988), even the type collection of J. Hall contains specimens of two unrelated taxa of different age. Their recommendation was that the name should not be used until the taxon was redefined. *T. longus* differs from the original description of *T. quadribrachiatus* in having a central disc in mature specimens. J. Hall (1865) noted that he had never seen one in *T. quadribrachiatus*. Also, the stipe divergence angles of *T. longus* are somewhat unusual, being more often below than above 90°. The great length of the stipes is also unique.

The number of specimens found might suggest that the species is a common one. This is not the case – it appears to be an invasion species, found covering surfaces in almost monotypic assemblages, and being very rare in intervening beds.



TEXT-FIG. 12. *Tetragraptus longus* sp. nov., PMO 97.708, Slemmestad. Illustration of part of a very big slab, showing ten (of a total of twelve) specimens with proximal part, and two pairs of very long stipes of the species, possibly both belonging to one specimen. The arrows point in the distal direction, and are placed along the ventral side of the stipe. Associated fauna is not shown.

Tetragraptus krapperupensis sp. nov.

Text-fig. 13A, C, E; cf. Text-fig. 13F

Name. From the Krapperup core.

Material. 6 specimens, all from the Krapperup core, three of them at 140·87 m, the other three at 140·30 m. Holotype LO 5988T (140·87 m; Text-fig. 13C), paratypes LO 5987t and LO 5989t (both from 140·30 m). One specimen of T. cf. *krapperupensis* (LO 5990t) is present at 129·46–129·54 m.

Associated species. A. murrayi, Didymograptus sp. 1.

Stratigraphic range. A. murrayi Zone, possibly also *H. copiosus* Zone.

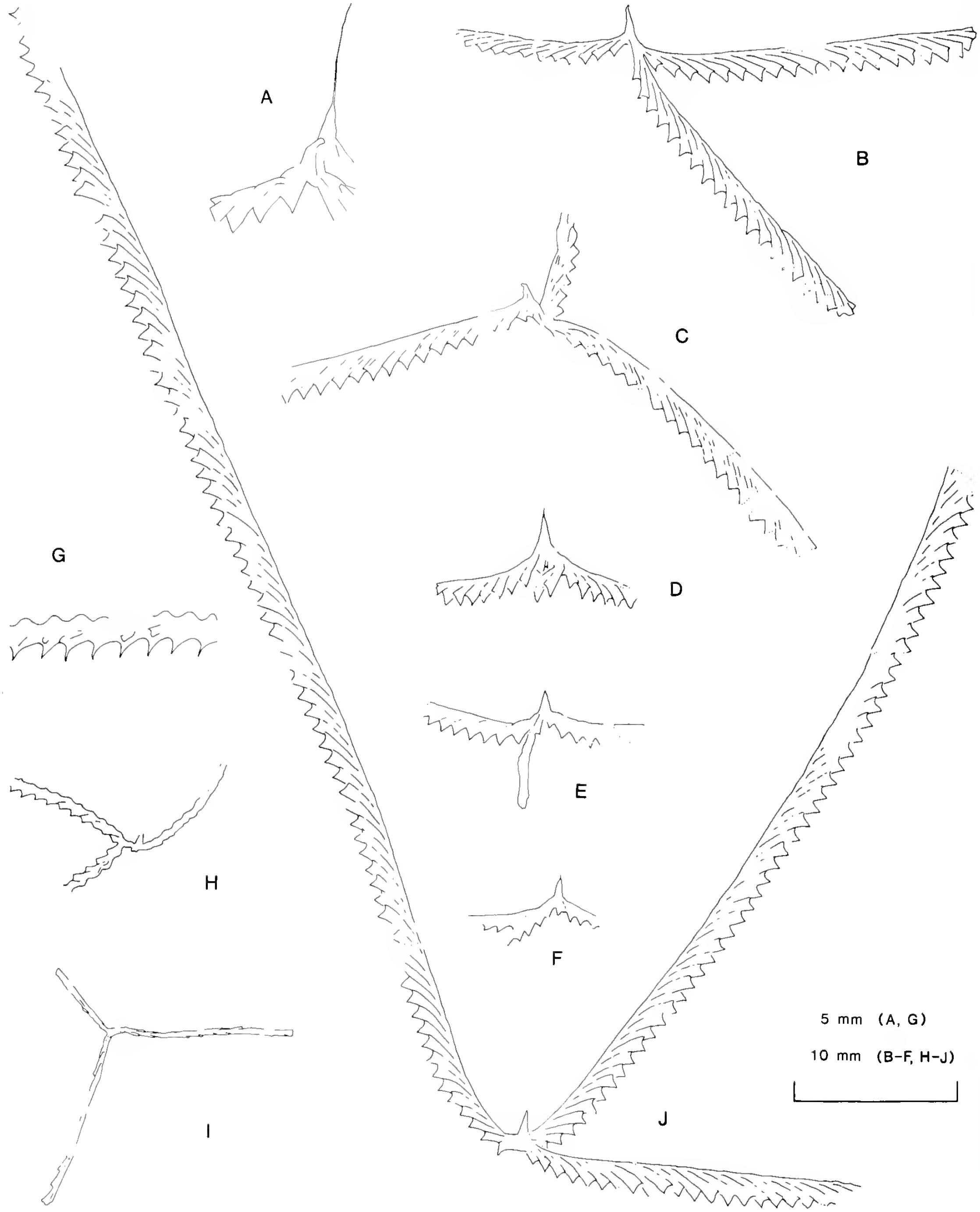
Diagnosis. A three-stiped species of slightly declined habit. Sicular length 2·2–2·5 mm, stipe width 1·3 mm proximally and up to 2·1 mm distally, 9·5–11 thecae in 10 mm, thecal overlap about one half, distal thecal inclination 35–45°.

Description. The sicula is 2·2–2·5 mm long and about 0·4–0·7 mm wide at the aperture. No specimen shows any details of proximal development. Only stipe^1 has a second dichotomy, after the first theca, resulting in 3 final stipes. The thecae are straight or slightly curved, about 2–3 times as long as wide. They are inclined at about 35–45° to the dorsal margin of the stipes. Well-preserved thecae are somewhat denticulate and have a concave aperture. The aperture is generally inclined at 60–70° to the dorsal margin of the stipes. The thecal overlap is mostly difficult to see, but appears to be approximately one half. There are 9·5–11 thecae in 10 mm, the lower value being found in the largest specimen. The proximal stipe width is about 1·3–1·4 mm, the maximum stipe width varies with the length of the stipes, from 1·5 mm in small specimens to 2·1 mm in the largest one. Across a specified theca the stipes are somewhat wider in larger specimens, possibly suggesting a certain amount of continued thecal growth. Two specimens (see Text-fig. 13A) indicate a plaited thecal structure – or triad budding: due to the relatively low relief, the presence or absence of bithecae along the stipes cannot be verified. The species could belong to the transitional forms with only traces remaining of an anisograptid structure (Lindholm and Maletz 1989). The stipes are declined in their proximal part. They are straight throughout or have a slight dorsally concave curvature. In life, the stipes were probably slightly declined.

One specimen, found a few metres higher in the core, has somewhat narrower stipes and more closely set thecae (Text-fig. 13F). Until more material of the species is known, I refer to it as *T.* cf. *krapperupensis.*

Remarks. No four-stiped rhabdosomes have been observed in the beds containing *T. krapperupensis* and the assignment of the species to the dichograptid form genus *Tetragraptus* is based on the fact that no bithecae have been identified, and that there are only two orders of dichotomy; there appears to be no other existing dichograptid genus for three-stiped forms. However, since preservation precludes observation of bithecae, these could in fact be present, in which case the species would have to be referred to an anisograptid genus. *Triograptus* is the only three-stiped anisograptid genus. It has three 'primary' stipes, i.e. the second-order dichotomy follows the first without intervening unicalycal theca (Cooper and Fortey 1983), although one specimen (Text-fig. 13H) in the collection forming the basis of Monsen's (1925) original description of the type species, *Triograptus osloensis*, appears to have two primary stipes, one of them branching after theca 1, just like the species here described. However, the thecal morphology of *Triograptus osloensis* (Text-fig. 13G) makes it very unlikely that the two species are closely related. Near the base of the Krapperup core there is one specimen probably belonging to another *Triograptus* species (Text-fig. 13I). Also this species has a thecal shape quite unlike that of *T. krapperupensis*.

Three-stiped rhabdosomes of roughly the same shape are found also in younger beds in southern Scandinavia. Five specimens were found with the *H. copiosus* fauna in Slemmestad (PMO 108.566, 108.569–108.570, 108.598; Text-fig. 13D). The thecal morphology agrees reasonably well with that of *T. krapperupensis*, but the sicula is much stouter and longer. This form is found together with four-stiped specimens. Three-stiped forms are especially common in the overlying *T. phyllograptoides* Zone (more than 150 specimens from Mt Hunneberg in RM, SGU, and Lund collections have been investigated), where three typical shapes can be seen among the declined to slightly reclined forms. Some additional specimens are preserved horizontally, so that thecal characteristics are obscured. This fauna has not yet been studied in enough detail to see if there is a continuous range of variation among its members or not, but it seems possible that there are distinct forms, some or all of which may be related to four-stiped forms, i.e. merit the name *Tetragraptus*. One form (Text-fig. 13B, J) is very similar in outline to *T. krapperupensis*. I hesitate to synonymize them since there are indications of a plaited thecal structure in *T. krapperupensis*, whereas specimens of the younger fauna have normal dichograptid stipes. Perhaps they formed part of a three-stiped lineage with separate bithecal reduction. Where three- and four-stiped specimens occur in the same beds it



TEXT-FIG. 13. *Tetragraptus krapperupensis* sp. nov. and comparative material. A, C, E, *T. krapperupensis* sp. nov., all from the Krapperup core; A, LO 5987t, 140·30 m, the left-hand stipe shows plaited thecal structure; C, holotype, LO 5988T, 140·87 m, the largest specimen; the drawing is a combination of counterparts; E, LO 5989t, 140·30 m, a smaller specimen with narrower maximal width. B, J, *Tetragraptus* sp. 1, Mossebo, Mt is often difficult to see if they are conspecific since the proximal parts of the four-stiped specimens tend to be preserved horizontally (dorsoventral view), so that the sicula and proximal width of stipes etc. cannot be seen.

Three-stiped rhabdosomes of various species appear to be present through most of the Arenig of southern Scandinavia. In the *T. phyllograptoides* Zone, in addition to the forms discussed above, there is a pendent three-stiped form which has no associated four-stiped pendent specimens. According to S. H. Williams (pers. comm.) it is identical to *P.* cf. *pendens* from Newfoundland (Williams and Stevens 1988). The Newfoundland fauna, however, contains both three- and four-stiped specimens. In beds above the *T. phyllograptoides* Zone in Scandinavia, practically all three-stiped forms have reclined rhabdosomes.

Some three-stiped forms from the *T. phyllograptoides* Zone at Mt Hunneberg were described by Maletz (1987) under the name of *T. triograptoides* (nomen nudum; junior homonym of *T. triograptoides* Harris and Thomas, 1938), but had been observed already by Törnquist (1904, pl. 1, fig. 20), who grouped them with four-stiped forms as *T. serra* (= *T. amii* according to current usage).

Non-triograptid, more or less horizontal, three-stiped forms of Tremadoc–Arenig age are known also from other areas. *Tetragraptus otagoensis* and *T. decipiens* (three-stiped form) from New Zealand were shown by Bulman and Cooper (1969) to have the same branching pattern as the Scandinavian forms. *T. otagoensis* is of La 2 zone age, and is therefore roughly coeval with *T. krapperupensis*, but has considerably narrower stipes than the latter. The three-stiped form of *T. decipiens* is somewhat younger, La 3 zone, approximately coeval with the *T. phyllograptoides* Zone fauna of Mt Hunneberg. It appears to have stipes narrower than the mature Scandinavian specimens, but it is worth noting that immature Scandinavian specimens, with stipes of comparable length to that of the New Zealand specimens, also have a comparable stipe width. As in the Scandinavian specimens, the second-order dichotomy in the New Zealand specimens is based on stipe^1 (the stipe developed on the th 1^1 side), quoted erroneously (R. A. Cooper pers. comm.) by Bulman and Cooper (1969) and Cooper (1979) as the stipe^2 side. The three-stiped form of *T. decipiens* has not yet been reported from Australia (R. A. Cooper pers. comm.).

Harris and Thomas (1938) described *Tetragraptus triograptoides* from the lowermost part of the Bendigonian of Victoria. This is a very slender form, belonging to the sigmagraptines, judging by its thecal characters. Chen *et al.* (1983) reported a specimen of a three-stiped extensiform species, *Adelograptus robustus*, from Jiangxi, South China, associated with *T. approximatus*. Its dimensions, apart from the comparatively broad proximal part of the stipes, are not far from those of certain specimens found at Mt Hunneberg, but it has bithecae along the stipes. A probably middle Arenig form was described from Czechoslovakia (*T. postlethwaitii*; Kraft 1987). It resembles the form illustrated in Text-figure 13B except in having slightly narrower stipes. The species contains both three- and four-stiped forms.

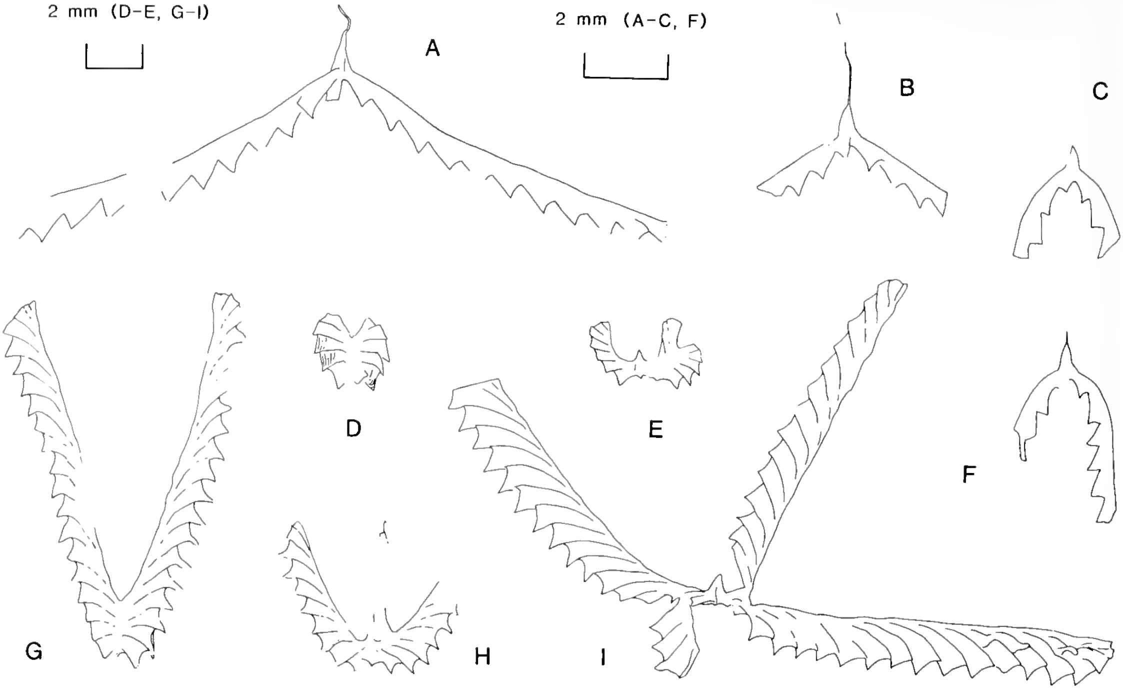
Form genus DIDYMOGRAPTUS M'Coy, 1851 (= DIDYMOGRAPTUS *s.l.*)

Didymograptus sp. 1

Text-fig. 14A, B

v cf. 1986 *Corymbograptus* sp. 1 Gutiérrez Marco, pp. 445–447, text-fig. 39D–M; pl. 14, figs 2, 4, 5.
v cf. 1988 *Didymograptus* cf. *sinensis* Lee and Chen; Molyneux and Rushton, p. 66, fig. 9*a*, *b*.

Hunneberg; B, SGU Type 8020; J, RM Cn 1838, the biggest specimen found. D, *Tetragraptus* sp. 2, PMO 108.569–108.570, Slemmestad; the drawing is a combination of counterparts. F, *T.* cf. *krapperupensis*, LO 5990t, Krapperup core 129·46–129·54 m. G–H, *Triograptus osloensis* Monsen, both on PMO 59.215, Stensberggaten, central Oslo, Ceratopyge Shale, 155–180 cm below the Ceratopyge Limestone; G, part of a stipe fragment showing shape of thecae; H, an aberrant specimen with two primary stipes and a second-order dichotomy. I, *Triograptus*? sp. 1, LO 6015t, Krapperup core, 151·45–151·46 m.



TEXT-FIG. 14. A, B, *Didymograptus* sp. 1, Krapperup core 137·72–137·76 m, two associated specimens; A, LO 5991t, the largest specimen found, slightly deflexed; B, LO 5992t, a seemingly declined specimen. C, F, *Didymograptus* sp. 2, Krapperup core, 118·50–118·54 m, two associated specimens; C, LO 5993t; F, LO 5994t. D, E, G, H, *Tetragraptus phyllograptoides* from near the base of the range of the species; all have considerably narrower stipes than the typical form; from two localities in the Slemmestad area; D, LO 5995t, immature *Phyllograptus*-like specimen, a–b pair; dotted circle indicates the broken connection towards the sicula; E, LO 5996t, a probably three-stiped specimen; the drawing is a combination of counterparts; G, LO 5997t, the largest specimen found, a–b pair; as in D, the connection towards the sicula is broken; H, LO 5998t, a probably three-stiped specimen showing few thecae in the conjoined part of the stipes. I, *Tetragraptus* sp. 3, PMO 112.967, 112.969, Slemmestad, associated with a *Hunnegraptus* fauna; a specimen in medium relief with the proximal part preserved as a mould; sicular outline drawn from counterpart.

Material. 10 specimens from the interval 147·33–137·70 m of the Krapperup core. Most specimens are small, showing no more than 4 thecae per stipe.

Associated species. A. murrayi, T. krapperupensis.

Stratigraphic range. A. murrayi Zone, and possibly higher beds.

Diagnosis. A thin (*c.* 0·7–0·8 mm) deflexed to declined didymograptid with sicular length about 1·4 mm and around 12 thecae in 10 mm. Thecae straight, inclined at *c.* 30°.

Description. All specimens are too flattened to show any details of proximal development or the possible presence of bithecae. The sicula is straight, 1·2–1·6 mm long and about 0·3 mm wide at the aperture. It protrudes about 0·7–0·9 mm above the dorsal margin of the rhabdosome. The thecae are almost straight tubes, inclined at about 30°. Their apertures are straight or slightly concave, inclined at 70–80 ° to the dorsal margin of the rhabdosome. There are normally 12 thecae in 10 mm, but the total variation seen is 11–14. The stipes are 0·6–0·7 mm wide proximally, widening to about 0·8 mm or, rarely, 1·0 mm distally. The shape of the rhabdosome is slightly deflexed or declined, with a stipe divergence angle of 120–145 °.

Remarks. The assignment of this species to *Didymograptus s.l.* is based on the fact that no bithecae have been seen along the stipes. Considering the age of the fauna, however, it is possible that bithecae are present, but not detectable due to the flattened state of the rhabdosomes. If so, the species will have to be referred to *Kiaerograptus*.

The general shape of the rhabdosome of this species is common to several species throughout higher parts of the Arenig and even the lower part of the Llanvirn, but the only similar species of roughly the same age are *Corymbograptus* sp. 1 Gutiérrez Marco, 1986, and *Didymograptus* cf. *sinensis* described by Molyneux and Rushton (1988). *Corymbograptus* sp. 1 differs only in having a somewhat shorter sicula and narrower proximal width, as well as a more accentuated deflexed shape in some of the specimens. *D.* cf. *sinensis* is, in my opinion, a synonym of that species, differing only in having slightly more thecae in 10 mm, well within the normal limits of variation of a species of that age. There are only a couple of reasonably large Swedish specimens, not necessarily representative of the mean of the population, hence further finds may prove the Swedish species to be conspecific with the Spanish/English one.

Gen. et sp. indet. 1

Text-fig. 11 E–H

Material. 4 specimens from Slemmestad crossroads, *c*. 0·5–1·0 m above the Ceratopyge Limestone, found on PMO 108.566, 108.567 and 108.599.

Associated species. *H. copiosus*, *Clonograptus s.s.* sp. indet., 3-stiped extensiform tetragraptids, *P. tenuis*, *P.* cf. *rarus*.

Stratigraphic range. *H. copiosus* Zone.

Diagnosis. A five-stiped rhabdosome, with a tetragraptid proximal part. Stipe width *c*. 1·6 mm, 9·5–11 thecae in 10 mm. A central disc is found in mature specimens.

Description. All four specimens are preserved horizontally, obscuring details of proximal morphology. The proximal part is tetragraptid, however, with one theca per first-order stipe. A well-developed central disc is found in the most mature specimens. The two largest discs measure 2 by 4 and 2 by 5 mm respectively (Text-fig. 11 F, H). The only specimen showing thecae in profile view (Text-fig. 11 G), has faint beginnings of a disc. The specimen is preserved in low relief and shows possible plaited thecal structure along one stipe (alternatively, it represents a compression structure). A characteristic of the species is that one of the second-order stipes divides consecutively. There are no indications in the available material of any further dichotomies, and it may be presumed that the final number of stipes is five, especially since there seems to be a certain amount of readjusting of the stipe angles, to even out the distances between the stipes. However, this is unfortunately difficult to prove due to the fragmentary state of the rhabdosomes. The thecae are slightly curved and somewhat expanded tubes, and slightly denticulate. The thecal overlap is about 60% and there are 9·5–11 thecae in 10 mm. The profile stipe width is 1·6 mm, the lateral width 0·5–0·7 mm.

Remarks. The three orders of stipes present in these specimens would suggest the use of the genus name *Dichograptus*. A reduction of the final stipe number is known to occur within *Dichograptus*. However, for the following reasons I prefer not to assign these specimens to that genus. Firstly, the Slemmestad form is older than any reported species of the genus and, secondly, I have not come across any definite *Dichograptus* specimens from the lower Arenig of Scandinavia. Additionally *Dichograptus* (as well as *Tetragraptus*) is likely to be a form genus and its type species, *D. sedgwicki*, has never been properly described (see Salter 1863; Elles and Wood 1902) and apparently has no associated fauna confirming its age. It was referred to as a subspecies of *D. octobrachiatus* by Elles and Wood (1902). Compared with *D. octobrachiatus*, the present form is much less robust and, due to the lack of details known from the proximal part of either taxon, their phylogenetic relationship is unclear. The beds containing my five-stiped form are of an age when great changes took place in the graptolite fauna, including not only the loss of bithecae along several lineages but, as far as I have seen, also an instability in the number of stipes present in a specimen. It thus seems more probable to me that the present form has a derivation separate from that of the later *Dichograptus* species.

Family SINOGRAPTIDAE Mu, 1957

Subfamily SIGMAGRAPTINAE Cooper and Fortey, 1982

Diagnosis (from Fortey and Cooper 1986): Dichograptinids with sigmagraptine proximal region.

Remarks. The Sigmagraptinae was originally described as a subfamily of the Dichograptidae with included species united by the characteristic proximal part and generally slender thecae. The taxon was raised to family rank by Fortey and Cooper (1986), consisting of the nominate subfamily only. Williams and Stevens (1988) lowered the rank back to subfamily level, and included it in the family Sinograptidae. I follow the classification of Williams and Stevens (1988), and also their concept of the content of the family (sinograptines, sigmagraptines, and the previously 'obscure' *Kinnegraptus*). The use of the name Sinograptidae follows priority rules, even though a sigmagraptid is the ancestor of the sinograptines.

The kinnegraptids were raised to family rank by Mu (1974) and were used at this level for *Paradelograptus* by Erdtmann *et al*. (1987). Also Williams and Stevens (1988), though temporarily including them in the Sigmagraptinae, considered the possibility that further study might show that the kinnegraptids merit family rank. However, my own investigations have shown them to be very close to the main stock of sigmagraptines. *Acrograptus gracilis* has an equally prolonged prosicula, and the exaggerated apertural lip (rutellum; Williams and Stevens 1988) of thecae and sicula is found among some of the *Paradelograptus* species, as well as in some specimens of *A. tenellus* (Hutt 1974, fig. 8A), the species which must be considered the best candidate for an ancestor of the Sigmagraptidae.

Genus PARADELOGRAPTUS Erdtmann, Maletz and Gutiérrez Marco, 1987

Diagnosis. See Erdtmann *et al*. (1987). The most important features mentioned are biradiality, irregular dichotomies, isograptid development, asymmetrical proximal part, and a characteristic thecal shape with long thin prothecae and expanding metathecae, sometimes provided with 'lappets' [here meaning *ventral* prolongation]. Bithecae were not observed.

Remarks. When defined by Erdtmann *et al*. (1987), the genus *Paradelograptus* was referred to the family Kinnegraptidae Mu, 1974. However, the authors base this family only on the shape of the thecae, disregarding features of the proximal end (1987, p. 113): 'This character [shape of the proximal part], however, is not a discriminating factor for *Paradelograptus* alone nor for the Kinnegraptidae and Sigmagraptinae [of the Dichograptidae], as was suggested by Cooper and Fortey (1982, p. 259), but it is observed quite frequently in many other dichograptids, dating back to the ancestral *Adelograptus tenellus* (Hutt, 1974, fig. 5B, Maletz and Erdtmann 1987) and to other adelograptinid forms (i.e. to *Choristograptus* Legrand, 1964). *Therefore, no taxonomic significance may be attached to this feature alone* [my italics]'. With this statement I disagree. In my opinion, they have defined a group of genetically related taxa. Further, figure 2 of Erdtmann *et al*. (1987), showing the 'phyletic relations' of taxa, disagrees with the text. The text states that the concepts of Cooper and Fortey (1982) have been used, that is, that Sigmagraptinae is a subunit of Dichograptidae. The figure, on the other hand, shows a possibly diphyletic Sigmagraptinae branching off the Kinnegraptidae, and possibly also the Clonograptinae.

Paradelograptus differs from *Adelograptus* solely in the absence of bithecae along the stipes. It includes both two-stiped and multi-stiped taxa. Among the *Paradelograptus* species described by Erdtmann *et al*. (1987) the proximal development is known only for the type species, *P. onubensis*.

It is quite possible that the genus *Paradelograptus*, with the constituent species as given by Erdtmann *et al.* (1987, p. 115; 15 species in all, those mentioned below and *P. sedecimus*, *P. rarus*, *P. smithi*, *P. ramulosus*, *P. chapmani*, *P.? tenuiramis*, *P.? clarkefieldi*, *P.? bulmani*, *C. tenellus* var. *problematica* Harris and Thomas, and *C. tenellus s.l.* Cooper and Steward), is a polyphyletic assemblage of similar-looking forms, which have responded in a similar way to peculiarities of the environment. However, the external shape of the proximal parts, with an adelograptid type of sicula, in *P. onubensis*, *P. antiquus*, *P. pritchardi* and *P. mosseboensis*, and *P. elongatus* and *P. tenuis* described here, is so similar as to make it likely that at least this group is monophyletic. *P. kinnegraptoides* appears from illustrations not to have an adelograptid sicula. The proximal development of *P. smithi* was not seen in the specimens from Mt Hunneberg, and the inclusion of that species by Erdtmann *et al.* (1987) seems to be based on thecal morphology alone.

Two new species are described here. A number of other species present in the Scandinavian Lower Hunneberg beds are mentioned under 'Other species' (p. 320).

Paradelograptus elongatus sp. nov.

Text-fig. 15C, G–I

Name. Latin *elongatus*, elongated, referring to the long first-order stipes.

Material. 16 specimens, 15 of which come from Slemmestad (14 of them on PMO 108.568–108.570, Slemmestad crossroads; 1 specimen, LR 2, from the base of the *T. phyllograptoides* Zone at Hagastrand, Lund collections). One specimen was found in the Krapperup core (124·87–124·89 m). A questionable specimen was found at Storeklev (2·32 m, Lund collections). Both the holotype (Text-fig. 15I; the only mature specimen) and the paratypes are found on PMO 108.570.

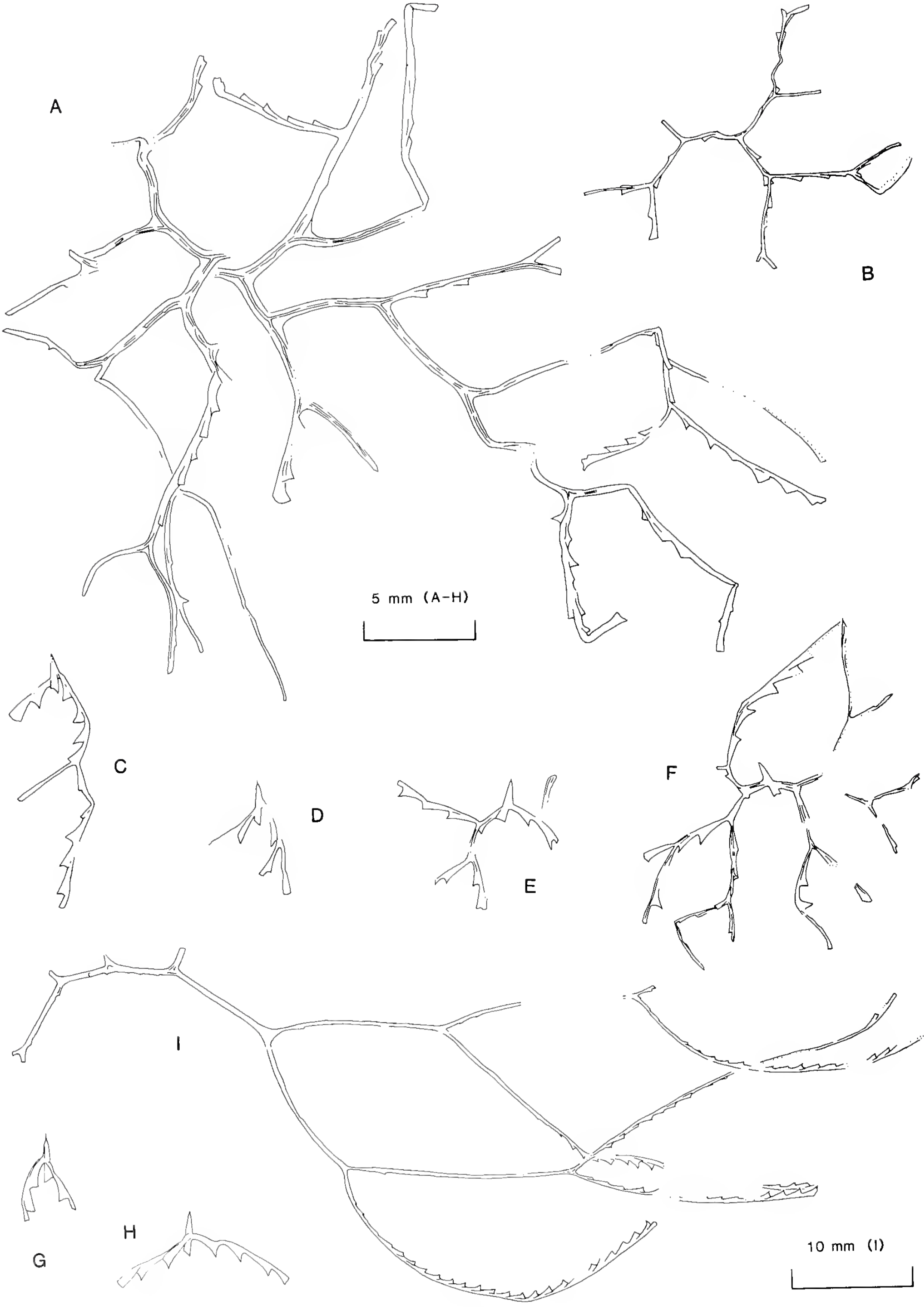
Associated species. A. murrayi, H. copiosus, P. antiquus.

Stratigraphic range. H. copiosus Zone, and at least the basal beds of the *T. phyllograptoides* Zone.

Diagnosis. Biradiate, declined to pendent in profile view, branching dichotomously at irregular intervals; first-order stipes consist of more than one theca. Proximal development probably isograptid; both sinistral and dextral forms occur. A sicular bitheca has been observed. Metathecae somewhat flared, but less so than in *P. mosseboensis*. Dimensions close to the latter.

Description. The sicula is straight and tube-like, 1·9–2·0 mm long and 0·3–0·4 mm wide at the aperture. Theca 1^1 originates close to the apex of the sicula. The development is probably isograptid, the prothecal part of th 2^1 is seen in the specimen in Text-figure 15G, and can be traced back almost to the point of origin of theca 1^2. A sicular bitheca is present on the obverse side of the sicula (Text-fig. 15C). There are both dextral and sinistral forms. The thecae are 2 mm long or longer, have relatively thin prothecal parts and somewhat flaring metathecae, which are sometimes seen to have a short denticle. Thecal width at the apertures reaches 0·4–0·5 mm. There are 8–9 thecae in 10 mm and the thecal overlap is about 40–50% (the point of origin of thecae is commonly obscure). The profile stipe width is 0·6–0·7 mm in proximal parts, up to 0·9 mm in distal parts. The first-order stipes vary in attitude from almost horizontal to pendent, if seen in profile view. The first dichotomy occurs at th 3 or later, sometimes considerably later: in one unbranched specimen, first-order stipes have 8 and 14 thecae. The holotype is a mature specimen showing five orders of stipes, the greatest number known. There is a considerable amount of cortical strengthening of proximal stipes in the holotype, giving it a much more rigid appearance than the associated smaller specimens. No bithecae have been observed along the stipes, but the material is mostly of low to no relief.

Remarks. P. elongatus most closely resembles *P. mosseboensis*, which occurs at a considerably higher level, around the lower boundary of the *D. balticus* Zone at Diabasbrottet, Hunneberg (Erdtmann *et al.* 1987, fig. 1). The dimensions of the two species are virtually the same, but the ventral thecal processes are less pronounced in *P. elongatus*. The latter is widely variable in the position of the second-order branching, whereas the corresponding range for *P. mosseboensis* was



TEXT-FIG. 15. For legend see opposite.

indicated as theca 2–3 (Erdtmann *et al.* 1987, p. 120). This range might be considerably wider, since the species was only represented by three incomplete specimens. The holotype of *P. elongatus* very much resembles that of *P. kinnegraptoides* in general shape, but not in size and thecal details.

Paradelograptus tenuis sp. nov.

Text-fig. 15A–B, D–F

? 1979 *Clonograptus tenellus* Linnarsson *s.l.*; Cooper and Stewart, pp. 785–786, text-fig. 8*m*.

Name. Latin *tenuis*, thin, small-sized.

Material. 15 specimens, 13 of which come from various localities in the Slemmestad area (12 of them, some with counterpart, are found on PMO 73.188–73.189, 73.191–73.192, 108.557–108.560, 108.566, 112.966–112.969, 113.031; one specimen, LR 3, from the base of the *T. phyllograptoides* Zone at Hagastrand, Lund collections). The other two specimens are from Storeklev (TUB HUN-S/2.18–2.3/006+030 and 036). Two additional questionable specimens from Storeklev were found on PU Vg 127 and one slab in the Lund collections (from 2·32 m). The holotype is a mature specimen on PMO 108.566 (Text-fig 15A), the four paratypes, all illustrated in Text-figure 15, are found on PMO 108.557–108.559.

Associated species. *A. murrayi*, *H. copiosus*, *C.* aff. *multiplex*, *Isograptus* sp., horizontal tetragraptids ('quadribrachiatus'-type).

Stratigraphic range. *H. copiosus* Zone and at least the basal beds of the *T. phyllograptoides* Zone.

Diagnosis. A small, thin paradelograptid with tetragraptid proximal part and frequent branchings. Sicula 1·6–1·9 mm long, 7·5–8 thecae in 10 mm, profile stipe width 0·5–0·65 mm, lateral width 0·2 mm or more.

Description. The sicula is of general paradelograptid shape, 1·6–1·9 mm long and 0·3–0·4 mm wide at the aperture. The two stipes diverge from the sicula at different levels, stipe^1 at sicular mid-length or slightly closer to the aperture, stipe^2 leaving 0·2 mm or less protruding on the ventral side of the stipe. The first-order stipes consist of one theca each (resulting in a tetragraptid proximal plan), the second-order ones of 1–3 thecae. The following orders each get a little longer, but in general aspect, the rhabdosome is very thin-stiped and rather densely branching. Six orders of stipes were found in the largest specimen.

The thecae have very low inclination, their ventral margins are concave, and they are denticulate. The apertural margins are straight to markedly concave, making an angle of 90° or more with the dorsal margin of the stipes. The profile stipe width is 0·5–0·65 mm and there are 7·5–8 thecae in 10 mm. The amount of thecal overlap could not be determined. The lateral stipe width is variable, 0·2–0·6 mm, depending above all on the amount of cortex overgrowth. A noticeable amount of cortex cover is only found in the most mature specimen where, due to slight pyritization, the outline of the stipes can be traced inside the cortex. No specimen was well enough preserved to verify presence or absence of bithecae. Badly preserved stipe fragments appear as thin branching 'threads' with no thecae visible.

Remarks. The size and shape of sicula and thecae are very close to those of *P. elongatus* (see Text-fig. 15). However, the two species differ in branching density and the position of the second dichotomy (tetragraptid proximal part only in *P. tenuis*).

TEXT-FIG. 15. A–B, D–F, *Paradelograptus tenuis* sp. nov., Slemmestad; A, holotype, PMO 108.566, the largest specimen, with considerable cortical thickening; B, PMO 108.557–108.558, horizontally preserved specimen; the drawing is a combination of counterparts; D, PMO 108.559, immature specimen with (secondarily?) pendent proximal part; E, PMO 108.557; F, PMO 108.559, combination of counterparts. C, G–I, *Paradelograptus elongatus* sp. nov., Slemmestad, all on PMO 108.570; C, specimen showing presumed sicular bitheca; G, H, specimens showing variation in proximal stipe attitude; I, holotype, the only mature specimen found; the sicula points downwards into the sediment, the two shortest second-order stipes point slightly upwards.

The general aspect of the species is very close to that of *C. tenellus s.l. sensu* Cooper and Stewart, 1979, from the La 2 zone of Victoria, Australia. The distal stipe width of *P. tenuis* is somewhat broader and, also, no cortical thickening was mentioned for *C. tenellus s.l.* There is a certain resemblance in shape also to *Adelograptus altus* Williams and Stevens (1991) but, due to the indifferent preservation of the mature specimens of that species and the generalized shape of the proximal part (similar to *P. elongatus*, *P. tenuis* and probably other species), no closer comparison can be made.

Other species

In the Early Hunneberg fauna there are several species in addition to the ones described above. Here, they are only briefly discussed as some of them are quite well known from other areas, others are hard to identify due to a fragmentary preservation, and still others are very rare and are not diagnostic of the fauna, e.g. horizontal tetragraptids.

Clonograptids s.l. Several specimens of a thin-stiped *Clonograptus* species with slightly prolonged first-order stipes (Text-fig. 10B) are present on PMO 97.708, from the Slemmestad area, together with *Tetragraptus longus* sp. nov. The species is very similar in outline to *Clonograptus rigidus*, but it appears to be thinner and the thecae are not well enough preserved for a definite identification.

Clonograptus (*Clonograptus*) aff. *multiplex* (PMO 108.557–108.559) occurs at Slemmestad and in the *T. phyllograptoides* Zone of Mt Hunneberg. It was described by Lindholm and Maletz (1989).

Robust stipe fragments probably belonging to *Clonograptus s.s.* (Text-fig. 10E) occur at a couple of levels low in the Krapperup core. A cortex-covered specimen was found in the Slemmestad area (PMO 113.032). It may belong to *Clonograptus norvegicus*.

Horizontal tetragraptids. These are extremely rare below the *T. phyllograptoides* Zone in the Krapperup succession: two very badly preserved specimens of tetragraptid outline ('quadribrachiatus'-type) were found at 152·89–93 m (LR 4–5), a level which probably equals a very early Hunneberg age. The longest stipe of the larger specimen is 15 mm. No thecal details are visible in this specimen, but a stipe of the other specimen, preserved in relief, seems to show a plaited thecal structure. Apart from this, only a possible immature specimen was found at 131·70–131·73 m.

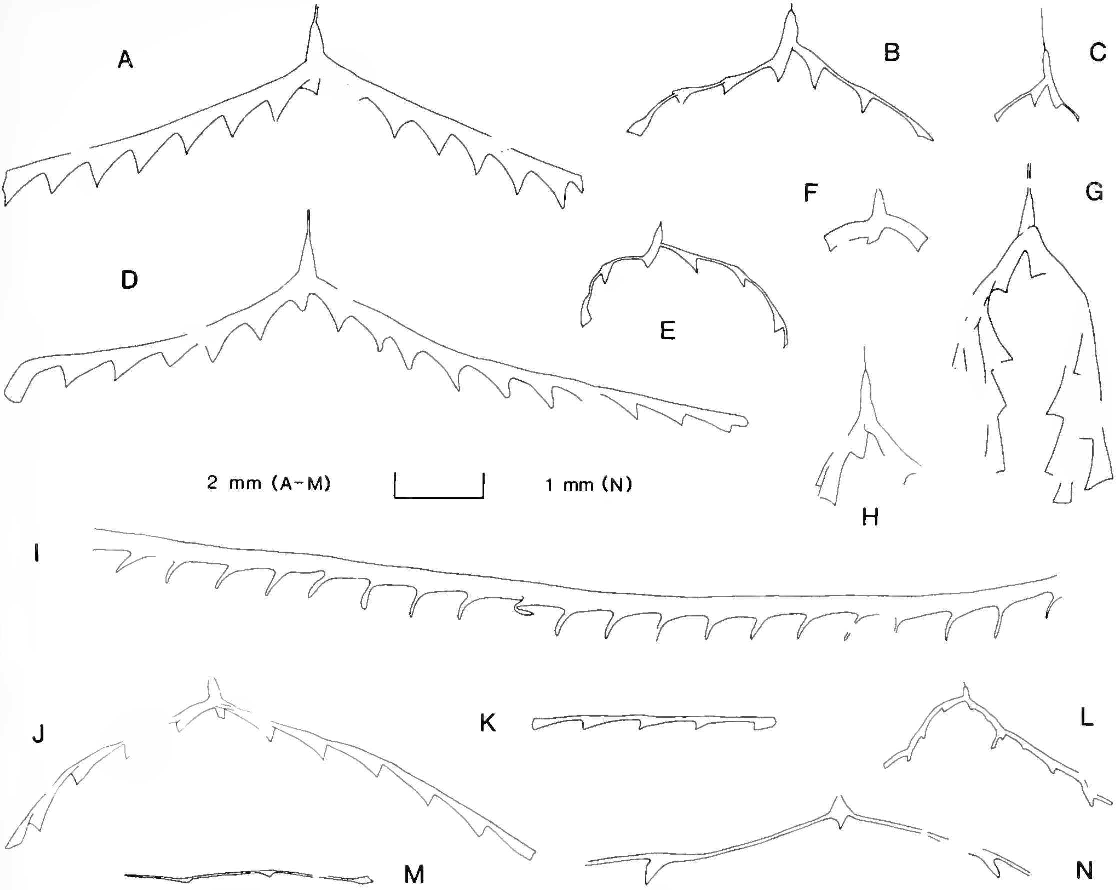
In the Storeklev section at Mt Hunneberg I have not found any tetragraptids. However, two specimens of '*Eotetragraptus* sp. 1' were reported by Maletz (1987; the stratigraphic level most likely corresponds to low *T. phyllograptoides* Zone). Thecal characters were not observable.

Tetragraptids are somewhat more frequent along with the *Hunnegraptus* fauna of Norway. Six specimens of varying stipe width have been found in the Slemmestad area (PMO 108.560, 108.569+108.570, 112.968, 112.969, 120.751, and one specimen in the Lund collections). Text-figure 14I illustrates the broadest specimen found. It is in moderate relief, but the irregularities seen in the lower right of the figure are hard to interpret: do they represent a plaited thecal structure or merely the effects of compression? A 3 mm wide stipe fragment of tetragraptid appearance was found on PMO 108.599.

Pendent didymograptids. A small pendent (or immature deflexed?) didymograptid species (Text-fig. 14C, F) has been found in the highest beds of the early Hunneberg fauna, just below the base of the *T. phyllograptoides* Zone. It is the most diagnostic species of this interval. It occurs at 118.54–112.75 m in the Krapperup core (47 specimens; the majority of them associated on a couple of surfaces and too badly preserved to form the basis of a description), and a few specimens were also found both at Mt Hunneberg and in the Slemmestad area.

Isograptids. Primitive isograptids have been found in the *H. copiosus* Zone in the Slemmestad area. These are apparently the oldest isograptids found anywhere. They will be described in a separate paper (Lindholm in prep.). The oldest specimens have isograptid symmetry, but much less reclined stipes than the majority of isograptids. They also possess a sicular bitheca. An additional specimen was found at 125.67–69 m of the Krapperup core.

Paradelograptids (Erdtmann *et al.* 1987). *Paradelograptus* is represented by several species, especially in the Krapperup core, see Text-figure 16.



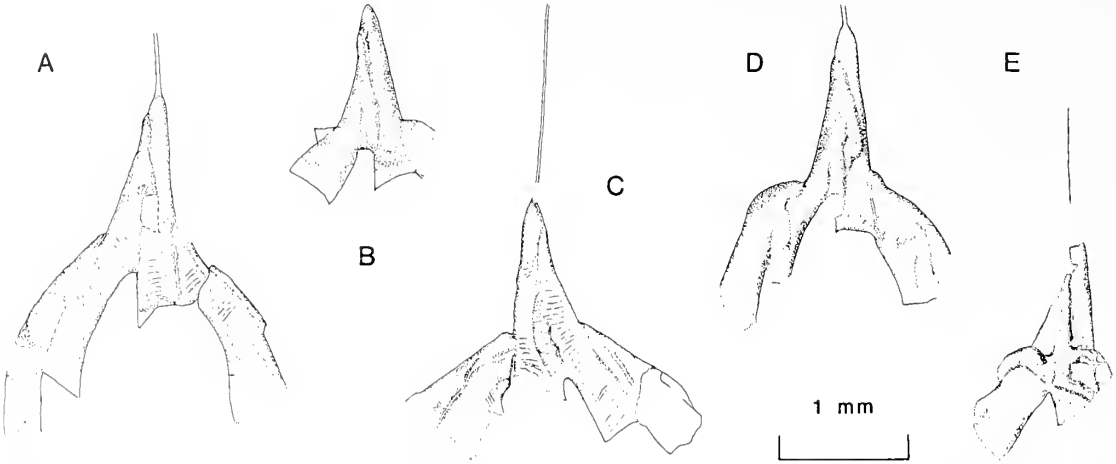
TEXT-FIG. 16. *Paradelograptus* species present in the topmost Tremadoc and lower Hunneberg of Scandinavia, but not described in this paper. A, D, *P. pritchardi* (T. S. Hall), two associated specimens, Krapperup core 134·20–134·26 m; A, LO 5999t; D, LO 6000t, the stipes are slightly twisted. B, *P. antiquus* (T. S. Hall), LO 6301t, Storeklev. C, *P.* sp. 1, PMO 112.967, Slemmestad. E, *P. onubensis* Erdtmann, Maletz and Gutiérrez Marco, LO 6001t, Krapperup core 151·46–151·50 m. F, *P.* sp. 2, LO 6002t, Krapperup core, 153·20–153·29 m. G, H, *P.* sp. 3, LO 6003t and 6004t, Krapperup core 151·96–151·99 m; the specimens are associated. I, *P.* cf. *rarus* (Harris and Thomas), LO 6302t, Storeklev. J, K, *P.* sp. 4; J, LO 6005t, Krapperup core 141·75 m; K, LO 6006t, Krapperup core 150·71–150·75 m. L, *P.* sp. 5, LO 6007t, Krapperup core 153·20–153·29 m. M, N, *P.* sp. 6; M, LO 6008t, Krapperup core 148·79 m; N, LO 6009t, Krapperup core 150·71–150·75 m.

One specimen of *P. onubensis* was found at 151·46–151·50 m. It is rather immature, with only two stipes, but the shape of the proximal part is unmistakable (Text-fig. 16E). A second specimen was found at 111·40–111·45 m.

P. pritchardi (Text-fig. 16A, D) occurs in the 135·09–118·50 m interval. *P. antiquus* (Text-fig. 16B) was found between 117·88 and 114·17 m of the Krapperup core. The species is also represented at Storeklev (LO 6301t, TUB HUN-S/2.18–2.3/023, PU Vg 124, and one specimen in the Lund collections), at Tøyen (GPI T4, T6), and at Slemmestad (PMO 108.568, 108.572, one specimen in the Lund collections).

Stipe fragments indistinguishable from *P. rarus* (Text-fig. 16I) were found at Storeklev (LO 6302t and counterpart; one specimen in the Lund collections) and Slemmestad (PMO 108.567, 109.148). Stipes probably belonging to the same species are not uncommon, but the thecal outline needed for identification is seldom seen.

In addition to these species, unidentifiable proximal parts and stipe fragments occur in the Krapperup core



TEXT-FIG. 17. Graptoloidea indet. spp. Relief specimens, all (and more) associated on one surface, near the base of the *A. murrayi* Zone, Krapperup core 147·66–147·72 m, LO 6010t–6014t. A–D show the sicular bitheca; D shows a bitheca in stipe 1. E could be interpreted as triradiate. C was drawn from a latex cast; E was combined from both counterparts. All illustrations were made under vertical light.

in the interval 153·29–134·20 m. Some of them are illustrated in Text-figure 16F–H, J–N. One of the species is minute – its sicula is only 0·3 mm long (Text-fig. 16M, N).

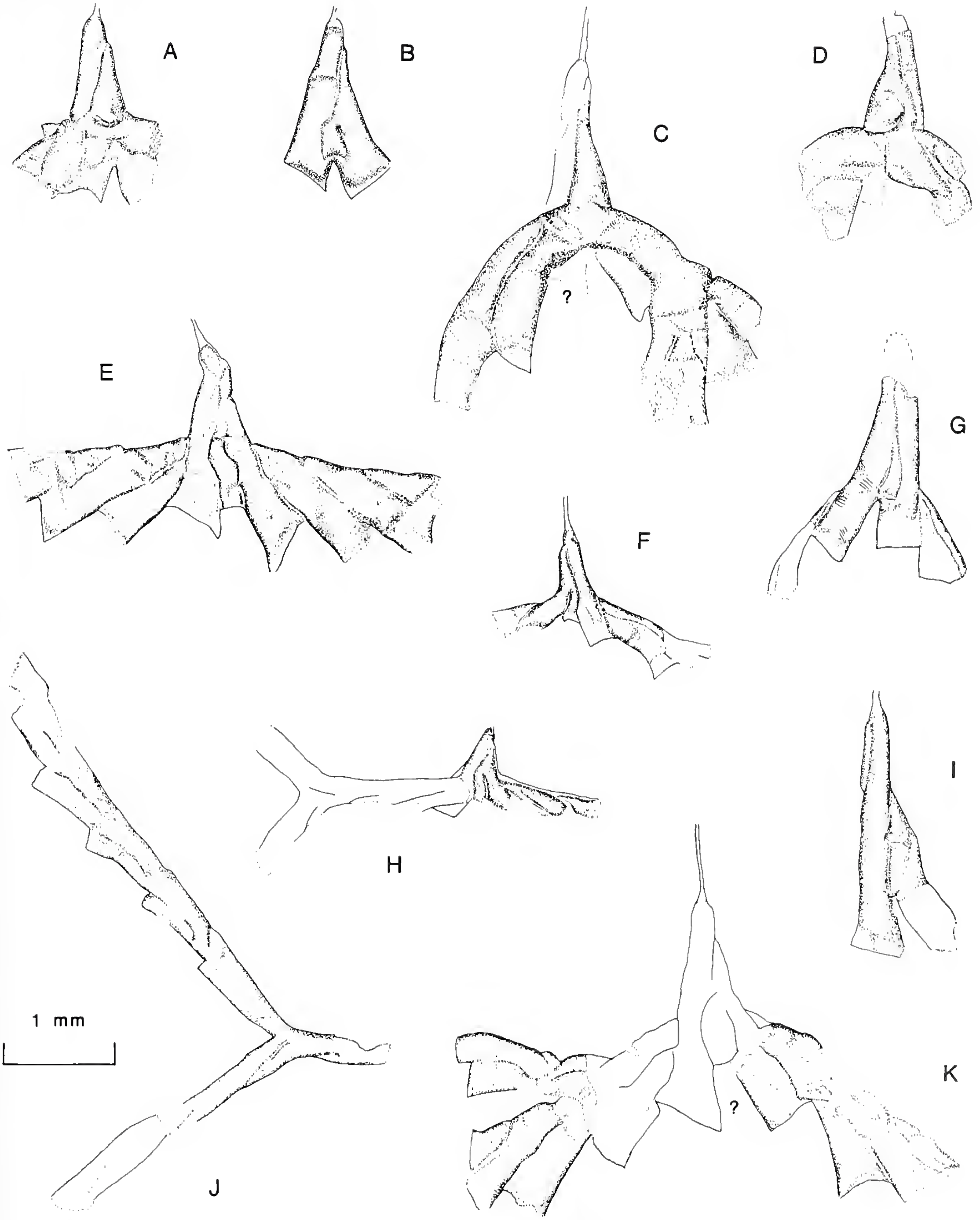
Relief specimens of unknown affinity. Text-figures 17 and 18 show some of the immature relief specimens of various kinds that have been found at two levels in the Krapperup core, 147·66–147·72 m and 132·63–132·66 m, i.e. close to the bases of the *A. murrayi* and *H. copiosus* Zones. At both levels all specimens in obverse view show a sicular bitheca. The stipes are mostly too incomplete to show presence or absence of bithecae. Specimens with bithecate stipes are present at the lower level (Text-fig. 17D), as well as possibly triradiate forms (Text-fig. 17E). The specimens are of extensiform, declined, and pendent types. Because stipes are incomplete, it is also difficult to say how many branchings the mature specimens would have had, but some of the pendent forms may belong to *A. murrayi* (Text-fig. 18C).

Kiaerograptids or didymograptids? The lower part of the Krapperup core, mainly below the level of the *Hunnegraptus* fauna, contains several badly preserved specimens that are declined to deflexed. They are seldom very big, mostly containing 5 thecae per stipe or less, but it seems unlikely that they would have branched further, had they lived longer. Because of their flatness (bithecae undetectable) and the short stipes (immaturity), their identity is uncertain.

The earliest T. phyllograptoides. This species does not belong in the fauna under discussion, but is present in the succeeding *T. phyllograptoides* Zone. It appears right at the base of its zone in Slemmestad, but some of the earliest specimens found there, in the lowermost metre, deviate from the typical form described by Cooper and Lindholm (1985). As seen in Text-figure 14E, H, some of the specimens could be three-stiped. Preparation gave no evidence of a fourth stipe. The atypical specimens also differ in having considerably narrower stipes (1·3–1·6 mm) and fewer thecae (2–4) in the conjoined part of the stipes. Only one specimen with normal width of stipes was found in the lowermost horizon at Grundvik, Slemmestad. Some specimens also have slightly less strongly reclined stipes.

So far, only 13 specimens (all belonging to the Lund collections) have been found this low, at three different localities, in the Slemmestad area: 3 specimens from 6·25 m above the Ceratopyge Limestone at Hagastrand; 8 specimens from 2·50 m above the missing part at Grundvik (*c.* 10 cm higher than Hagastrand) and one specimen 12 cm higher; finally one specimen from about 80 cm higher than the lowest Grundvik level at the Rortunet section.

In the Krapperup core, some weakly reclined tetragraptids are found a couple of metres below the first find of *T. phyllograptoides*. They are mostly very short-stiped, and no species identification has been attempted.



TEXT-FIG. 18. Relief specimens, all (and more) associated on one surface, near the base of the *H. copiosus* Zone, Krapperup core, 132·63–132·66 m, LO 6085t–6095t. A, B, D, E, G, I, K, Graptoloidea indet. spp; B shows a typical symmetrical pair formed by the sicula and th 1^1, with the bitheca in the centre; E has no bithecae along the stipes; I shows th 1^1 growing around the sicula; in K, the proximal part is a mould; all specimens in obverse view show a sicular bitheca. C, ?*Araneograptus murrayi* (J. Hall), the stipes are of dichograptid type. F, J, *H. copiosus* sp. nov. H, cf. *H. copiosus*; the apex of the sicula points somewhat downwards. J and K were made from latex casts, C and E from combinations of counterparts. All illustrations were made under vertical light.

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TRILOBITES FROM THE ORDOVICIAN OF PORTUGAL

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ABSTRACT. The following trilobite species from the Llanvirn to Llandeilo of north and central Portugal are recorded or described and their stratigraphical ranges are discussed: *Colpocoryphe* aff. *rouaulti* (Henry), *C.* cf. *thoralis conjugens* Hammann, *C. grandis* (Šnajdr), *Salterocoryphe salteri salteri* (Rouault), *Prionocheilus mendax* (Vaněk), *P.* cf. *pulcher* (Barrande) and *Valongia wattisoni* (Curtis). *Actinopeltis tejoensis* sp. nov. and *Prionocheilus costai* (Thadeu) from the upper Ordovician of central Portugal are described. *Salterocoryphe lusitanica* (Thadeu) is put into synonymy with *Salterocoryphe salteri salteri*; *Prionocheilus* cf. *pulcher* is recorded for the first time from Portugal; authorship of *Prionocheilus costai* is here attributed to Thadeu and a lectotype is chosen. The faunas show similarities with those in central Iberia and northwest France.

CALYMENID, cheirurid and bathycheilid trilobites form an important element of the Ordovician faunas of Portugal. As early as 1849, Sharpe noted the presence of '*Calymene Tristani*' and '*Cheirurus*' from Valongo (Text-fig. 1), and some years later Ribeiro (1853) recorded '*Calymene Tristani*' and '*Calymene Arago*' from Buçaco. Delgado (1897, p. 28; 1908, pp. 57, 80, 106) listed six species of '*Calymene*' from the Ordovician of Buçaco, Amêndoa/Mação and Valongo, but did not describe or figure any of the material. Subsequently, Costa (1942) published a short account on the Calymenidae in which he figured '*Calymene Tristani*' and '*Calymene Salteri*' from Valongo. More recently Thadeu (1947) revised some of the upper Ordovician trilobites from Buçaco, among which he described and figured the following species of '*Cheirurus*': '(?)*Bocagei*, *claviger*, *gelasinosus*, (?)*Venceslasi*, aff. *completus* and aff. *verrucosus*', as well as '*Pharostoma costai*'. Two years later Thadeu (1949) revised the Portuguese calymenids and recognized five species of '*Synhomalonotus*' ('*Aragoi*, *Salteri*, *Tristani*, *transiens*, *lusitanica*') and two of '*Pharostoma*' ('*Costai*, *pulchra*'). South of the River Douro, along an extension of the Valongo outcrops, Thadeu (1956) again recorded the species '*aragoi*' and '*tristani*', as well as '*Calymeme* cf. *duplicata*'. Curtis (1961) described *Actinopeltis wattisoni* from the Valongo area.

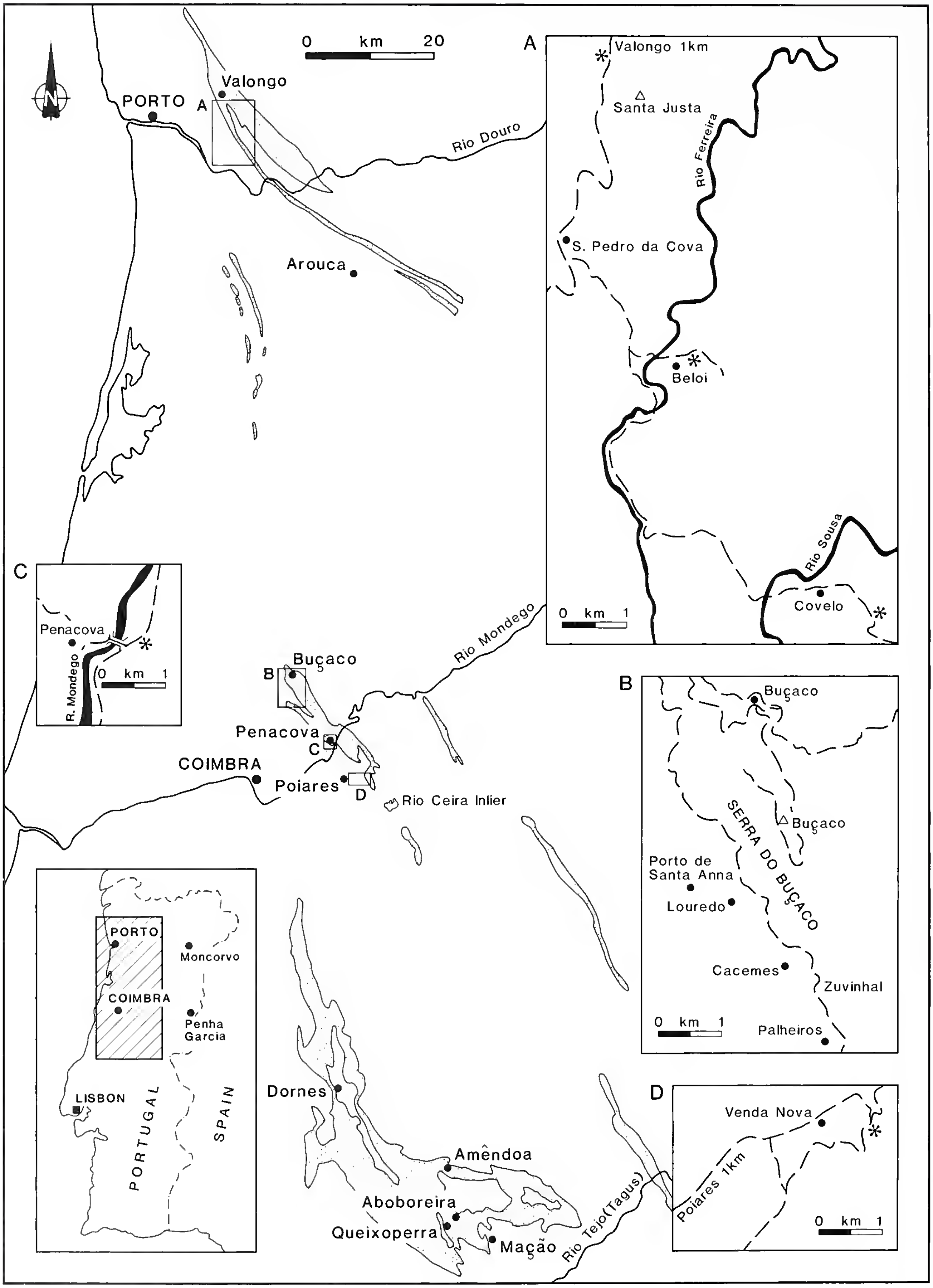
The present paper revises the taxonomy and distribution of the following genera from the Ordovician of Portugal: *Colpocoryphe*, *Salterocoryphe*, *Prionocheilus*, *Actinopeltis* and *Valongia*. Most of the material is restricted stratigraphically to beds of Llanvirn to early Caradoc age; only *Prionocheilus costai* (Thadeu, 1947) is of late Caradoc–?Ashgill age.

Material used is housed in the collections of the Geological Survey offices, Lisbon (prefixed SG or MR) and Earth Sciences Unit, University of Sheffield (prefixed P or RC). Further material was kindly made available by Dr A. H. Cooper (Cooper 1980) and Dr T. P. Young (Young 1985; prefixed ABO, CST, LOR, MDC, PEN, PG and QXP, at present in the Geology Department, University College of Cardiff).

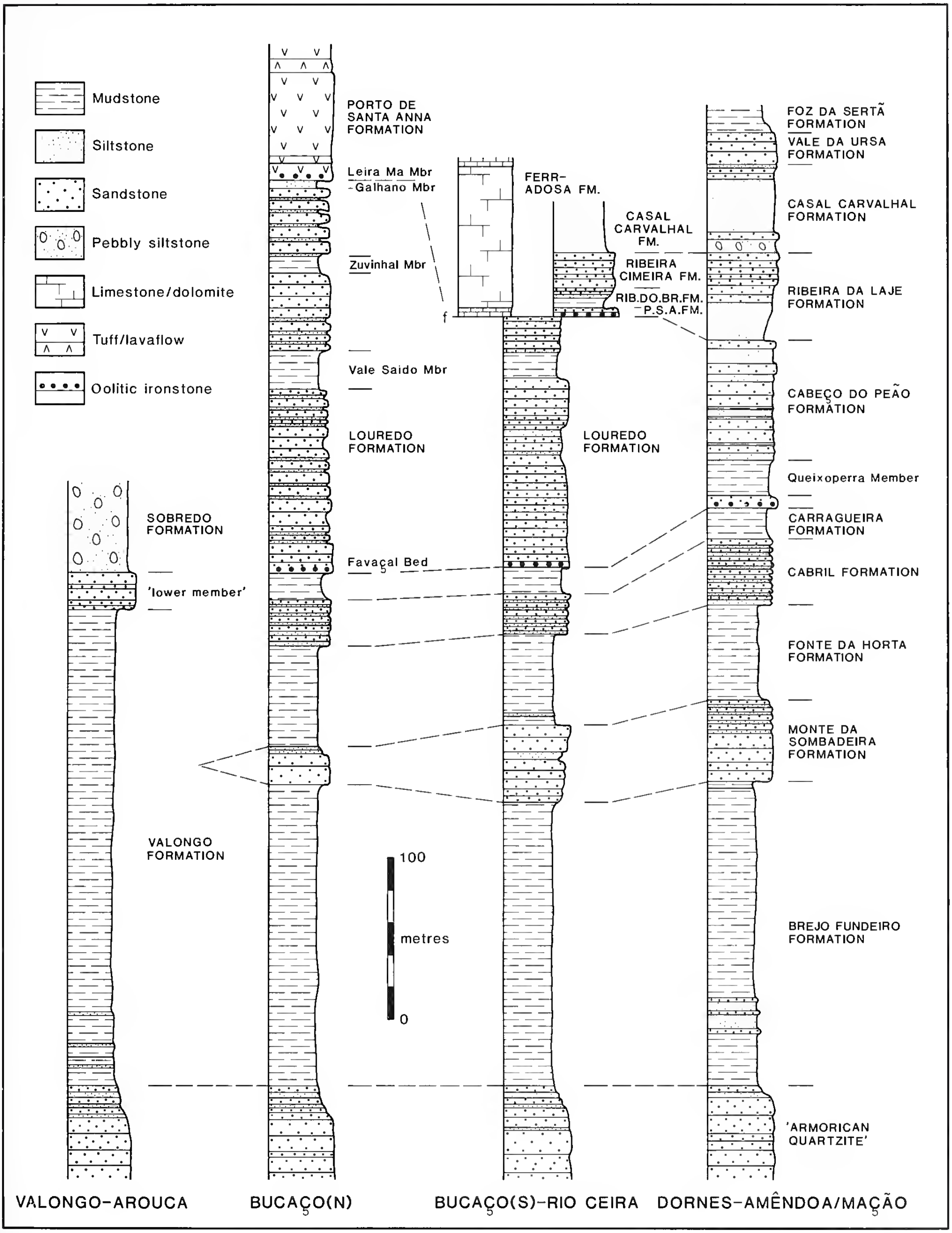
STRATIGRAPHY

The material studied is mainly from the major outcrops of fossiliferous rocks in Portugal; namely Valongo to Arouca, Buçaco to Rio Ceira, and Dornes to Amêndoa/Mação (Text-fig. 1). The simplified stratigraphic columns in Text-figure 2 illustrate the major lithotypes, formations and members of these regions. More detailed descriptions of the rock units may be found in Romano

[Palaeontology, Vol. 34, Part 2, 1991, pp. 329–355, 4 pls.]



TEXT-FIG. 1. Location maps of north and central Portugal, showing fossil localities mentioned in the text.



TEXT-FIG. 2. Generalized lithostratigraphic sections for north Portugal (Valongo-Arouca) and central Portugal (Buçaco, Buçaco-Rio Ceira, Dornes-Amêndoa/Mação).

and Diggens (1976), Henry, Nion *et al.* (1976), Mitchell (1974), Cooper (1980), Brenchley *et al.* (1986) and Young (1985, 1988).

A brief resume is given here of the successions shown in Text-figure 2. The Llanvirn–Llandeilo sequence at Valongo to Arouca is a monotonous sequence of mudrocks overlying the Armorican Quartzite. The mudrocks (Valongo Formation) are abruptly succeeded by quartzites, above which are pebbly siltstones and sandstones of the Sobredo Formation. This latter unit is of glaciogenic origin and is probably of late Ordovician (Hirnantian) age. The region between Buçaco and Rio Ceira shows a general homogeneity and differs significantly in detail from the Valongo sequence. Young (1985, 1988) has recently revised the lithostratigraphy of this region above the Monte da Sombadeira Formation (Brenchley *et al.* 1986) and his terminology is incorporated in Text-figure 2. Graptolitic mudstones of Llanvirn age are known from the Brejo Fundeiro Formation (Cooper 1980) and diverse Llandeilo faunas occur in the Fonte da Horta Formation. The base of the Llandeilo is within the upper part of the Brejo Fundeiro Formation, and the Carregueira Formation is probably of early Caradoc age (Young 1988). The Louredo Formation is entirely Caradoc in age; the fossiliferous basal Favaçal Bed is considered to be of early Caradoc age (Henry and Thadeu 1971; Henry, Nion *et al.* 1976; Paris 1979, 1981), while the faunas from the uppermost mudstone unit (Galhano Member) indicate an upper Caradoc age (Paris 1979, 1981; Young 1988). The overlying Porto de Santa Anna Formation contains a rich fauna in the basal Leira Ma Member. Mitchell (1974) attributed an early Caradoc age to this assemblage but later authors have suggested a late Caradoc/early Ashgill age. Young (1988) suggested a possible Rawtheyan age for the upper part of the Porto de Santa Anna Formation. In the southern part of the Buçaco to Rio Ceira region the Porto de Santa Anna Formation is replaced by a sequence of massive dolomites; in the extreme south around Rio Ceira, clastic sequences overlie an attenuated Porto de Santa Anna Formation and are succeeded by pebbly siltstones of the Casal Carvalhal Formation.

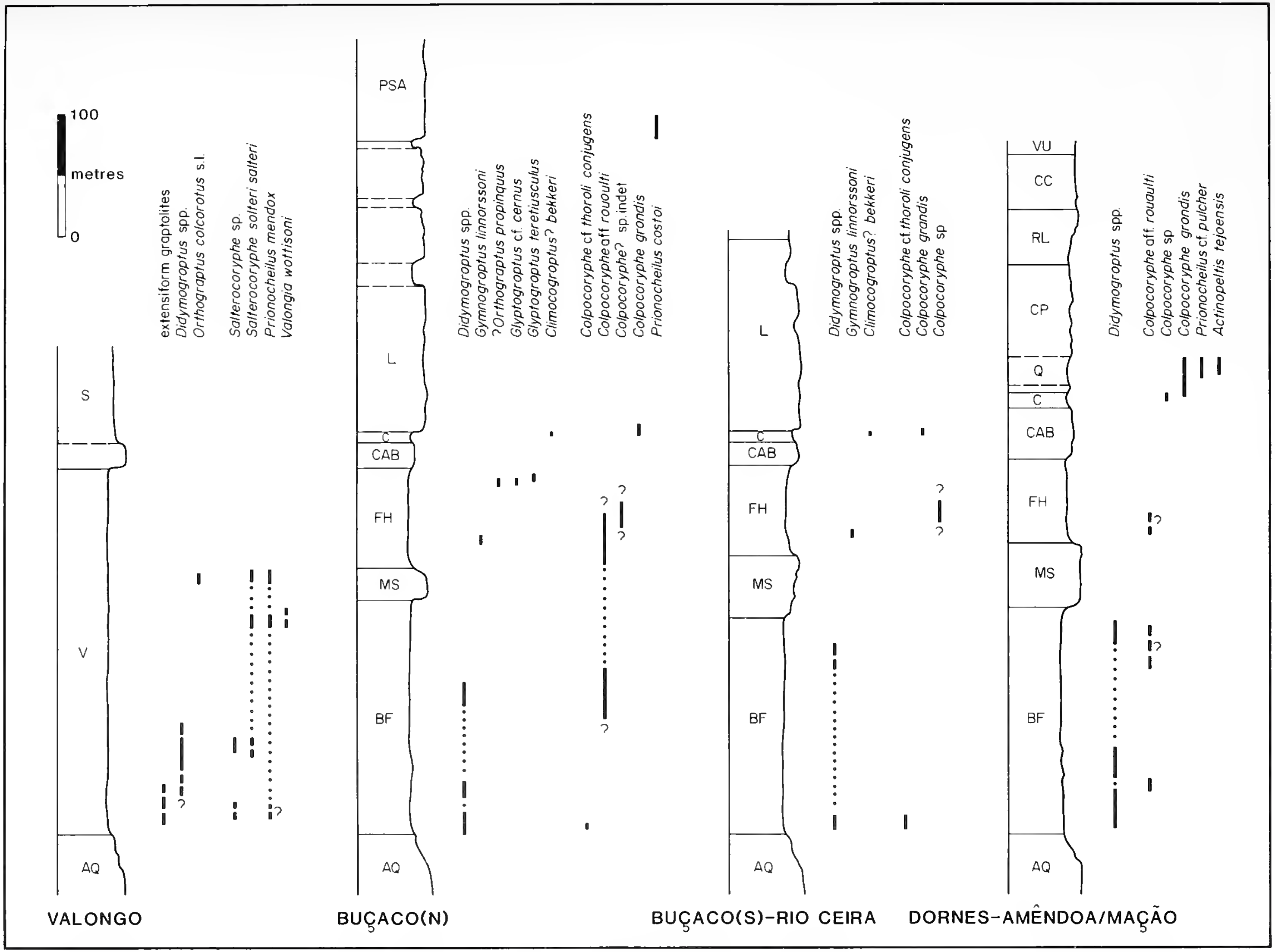
The final column in Text-figure 2 represents the sequences around Dornes and Amêndoa/Mação. The units here, up to the Favaçal Bed, are essentially similar to those around Buçaco. In the lower part of the Cabeço do Peão Formation, however, is a richly fossiliferous unit, termed the Queixoperra Member (Young 1988), of early Caradoc age (includes the Bryozoa Beds of Cooper 1980). Poorly fossiliferous sequences overlie the Cabeço do Peão Formation in this southern region, but the pebbly siltstones of the Casal Carvalhal Formation may be correlated with those of the Rio Ceira section and probably the Sobredo Formation at Valongo. The upper part of the Vale da Ursa Formation (Cooper 1980; Young 1988) contains graptolites indicating an early Llandovery age.

REMARKS ON THE VERTICAL RANGES AND GEOGRAPHICAL DISTRIBUTIONS OF THE TRILOBITE FAUNAS

Vertical ranges

Colpocoryphe aff. *rouaulti* Henry, 1970. This species is first known from the upper Llanvirn where it is present approximately 30 m above the top of the 'Armorican Quartzite' in the Dornes area (Cooper 1980) and persists at least into the Lower Llandeilo (Text-fig. 3). A broadly similar range is known for *C. rouaulti* in Spain (Hammann 1983; Gutiérrez-Marco *et al.* 1984), and in Brittany it is known to occur from the upper Llanvirn to the *Marrolithus bureaui* biozone (Henry 1980*a* and pers. comm.) where it is common south of Rennes (Traveusot Formation) but rare in the upper part of the Postolonnec Formation in the Crozon Peninsula (Henry 1980*a*).

Colpocoryphe cf. *thorali conjugens* Hammann, 1983. This species first appears less than one metre above the Armorican Quartzite Formation in the Buçaco syncline where it is of early Llanvirn age (Romano *et al.* 1986); its upper range limit has not yet been established in Portugal. In northeast Portugal it has been recorded from near Moncorvo (Text-fig. 1) in beds low down in the Xistenta Formation (Rebelo and Romano 1988) where it is probably of Llanvirn age. Thadeu (1956, p. 19, pl. 6, fig. 1) recorded *C. aragoi* from the Canelas quarries at Arouca, south-east of Valongo. The specimen figured by Thadeu is poorly preserved but Henry (1970, p. 13) tentatively assigned it to



TEXT-FIG. 3. Sections showing ranges of graptolite and trilobite species. Abbreviations refer to lithostratigraphic units shown in Text-figure 2.

C. rouaulti. I have not seen Thadeu's specimen but have collected further material from the quarries which include *Salterocoryphe* sp. (possibly *S. salteri salteri*). Thadeu mentioned the presence of furrows on the pleural lobes of the pygidium of the Arouca specimens which suggests that it may be better assigned to *Salterocoryphe*; the details of the preglabellar area are not easy to distinguish from Thadeu's figure but the apparently bell-shaped glabella is reminiscent of *S. salteri salteri*. The age of the Canelas quarries assemblage was regarded as Llandeilo by Thadeu but the presence of *Hungioides bohemicus* (see Rábano 1983), *Bathycheilus*? *castilianus* and *Nobiliasaphus caudiculatus*, as well as poorly preserved pendent didymograptids, suggests a Llanvirn and possibly early Llanvirn age (Gutiérrez-Marco *et al.* 1984). Courtessole *et al.* (1981) assigned *C. thorali thorali* (Dean, 1966), from the Lower Arenig of the Montagne Noire, to *Salterocoryphe* but this is not accepted here.

Colpocoryphe grandis (Šnajdr, 1956). This species in Portugal appears to be restricted to the lower Caradoc and first makes its appearance in the Carregueira Formation in central Portugal. It is last recorded from the Queixoperra Member of the Cabeço do Peão Formation, some 15–20 m above the Favaçal Bed. The species has a greater stratigraphic range in Brittany (Henry 1980*a*) where it is known from the top of the Postolonnec Formation, Schistes de Raguenez and Riadan Formation. In Spain, Rábano (1984) records it only from the Caradoc but I have collected a deformed cephalon of *Colpocoryphe* from just above the Los Rasos sandstones (equivalent to the Monte de Sombadeira Formation) in the Guadarranque area, Toledo Mountains, central Spain, which is very close to *C. grandis*. Hammann (1983, unit 6 in Guadarranque section) considered this horizon to be of Llandeilo age and, if the identification proves to be correct, thus possibly extends the range of this species in Spain to approximately equal to that in Bohemia, where it is of Llandeilo–Caradoc age (Dobrotivá, Libeň and Letná Formations, see Havlíček and Vaněk 1966).

Salterocoryphe salteri salteri (Rouault, 1851). This species definitely occurs in beds of Llandeilo age from the upper part of the Valongo formation in north Portugal, but as yet I have not recorded undoubted specimens from the Llanvirn. However, at Arouca, a single pygidium from the lower part of the Valongo Formation (probably early Llanvirn) is tentatively identified as *S. salteri salteri*. Delgado (1908, pp. 134, 137 and 138) questionably identified the species from the 'Schistes à *Didymograptus*' (lower part of the Valongo Formation and considered by Gutiérrez-Marco, *fide* Hammann *et al.*, 1986 to be of early Llanvirn age), but this material has not been seen by the author. In Spain the species occurs in the Llanvirn at Guadarranque and much of the Llandeilo of Corral de Calatrava and El Centenillo (Hammann 1983; Gutiérrez-Marco *et al.* 1984), while in Brittany it appears to be restricted to the Llandeilo (Henry 1980*a*) where it occurs south of Rennes, on the northern flank of the Laval syncline and only very rarely in the western part of the median syncline.

Prionocheilus mendax (Vaněk, 1965). The range of this species in Portugal parallels that of *S. salteri salteri*; it is of Llandeilo age at Valongo but possibly extends down into the Llanvirn (Delgado 1908, pp. 57, 106). In Bohemia it ranges from the Llandeilo to lower Caradoc (Vaněk 1965) while in central Spain and Brittany it is exclusively of Llandeilo age (Rábano 1984; Henry 1980*a*).

Prionocheilus cf. *pulcher* (Barrande, 1846). This species has so far only been recorded from the Caradoc of the Dornes–Amêndoa/Mação region and as far as I am aware does not occur in Spain. In Brittany it has only tentatively been recorded from the lower Caradoc although Dr J.-L. Henry informs me that there are differences in that the French specimen shows shorter and straighter spines on the cephalic border than either *P. pulcher* or *P. verneuili*. In Bohemia it has a range throughout much of the Caradoc.

Prionocheilus costai (Thadeu, 1947). This species in central Portugal is so far only known from beds of late Caradoc or early Ashgill age and is probably of a similar age in Spain (Hammann 1983) where it is known from the 'Bancos mixtos'. It is also present in dropstones from the basal part of the Casal Carvalhal Formation at Dornes (Dr T. P. Young pers. comm.). In Brittany it occurs in the lower part of the Rosan Formation.

Actinopeltis tejoensis sp. nov. This species is only known from the Queixoperra Member, Amêndoa/Mação region, of Caradoc age. The genus is recorded from Spain, from the Caradoc (Hammann 1972; Rábano 1984), and also from the Rosan Formation of Brittany (J.-L. Henry pers. comm.).

Valongia wattisoni (Curtis, 1961). This monospecific genus is at present only known from the Llandeilo of Valongo.

Geographical distributions

The distribution of the species described in this paper substantiates the previously documented contrast found in the composition of the trilobite faunas in north (Valongo–Arouca, Marão, ?Moncorvo) and central (Buçaco–Amêndoa/Mação) Portugal throughout much of the Ordovician (Hammann and Henry 1978; Henry and Romano 1978; Romano 1982). For example, during the lower Llandeilo *Salterocoryphe salteri salteri*, *Prionocheilus mendax* and *Valongia wattisoni* are only known from the 'northern' region, while *Colpocoryphe* aff. *rouaulti* is apparently restricted to the 'southern' region (although an imperfectly preserved specimen of ?*Colpocoryphe* is known from the upper part (Llandeilo) of the Valongo Formation in the north). During Caradoc–Ashgill times, trilobite faunas are at present unknown in north Portugal but *C.* aff. *rouaulti*, *C. grandis*, *P.* cf. *pulcher*, *P. costai* and *A. tejoensis* occur further south. However, in the lower Llanvirn, *C.* cf. *thorali conjugens* appears to have had a wider distribution and is recorded from Moncorvo and Buçaco–Rio Ceira.

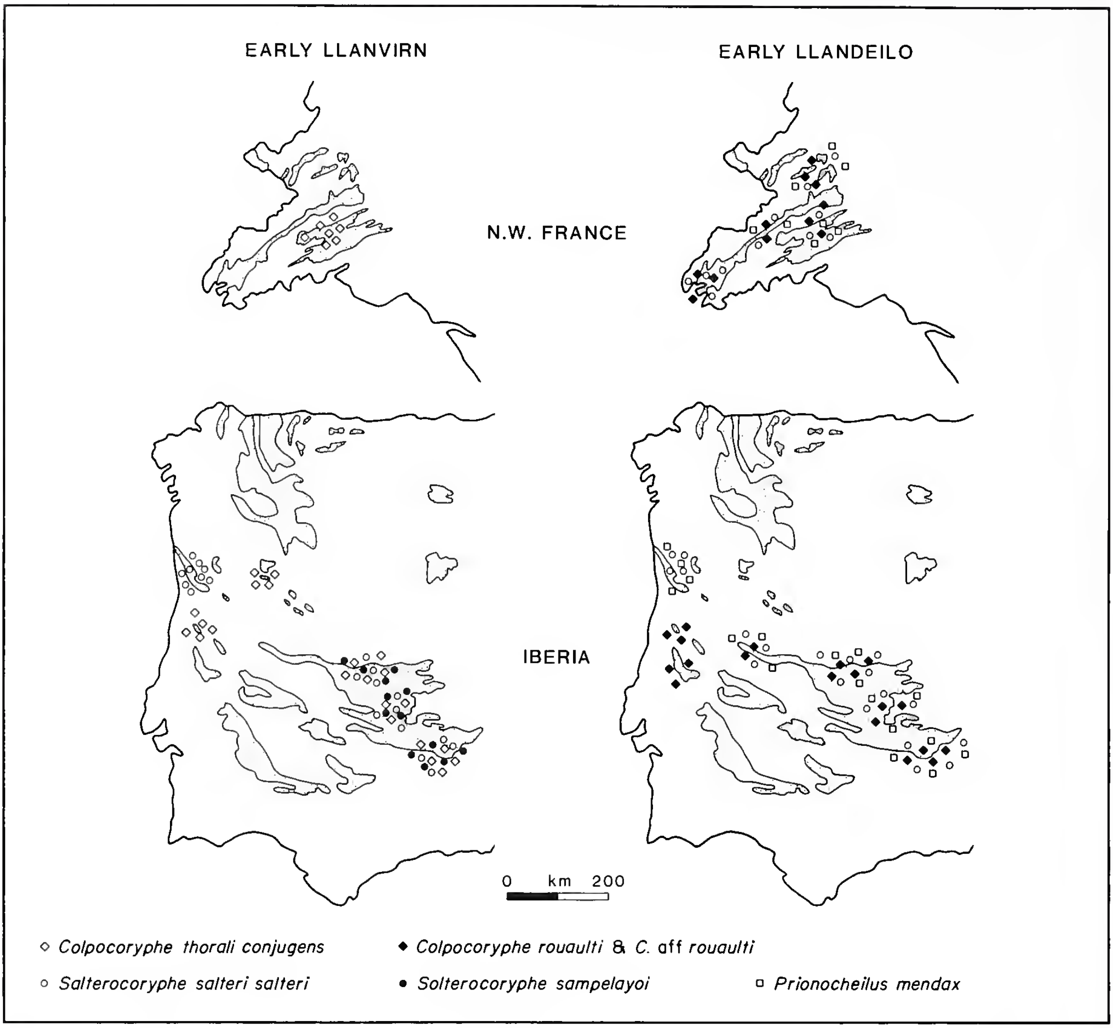
Within Brittany and Spain, trilobite associations also show restricted distribution (Henry 1980*a*; Rábano 1984) and it has been frequently noted that, for example, sequences and faunas in the Crozon Peninsula have more in common with the Buçaco area in Portugal (Henry and Thadeu 1971; Paris 1981; Young 1989, 1990) than with the Ordovician succession south of Rennes (Henry and Morzadec 1968; Henry, Mélou *et al.* 1976; Henry, Nion *et al.* 1976).

Two maps are presented (Text-fig. 4) of France and Iberia during early Llanvirn and early Llandeilo times which show the distribution of the trilobites described in this paper. These distributions are now briefly discussed.

Early Llanvirn. C. thorali conjugens, *S. salteri salteri* and *S. sampelayoi* are known to occur in the Montes de Toledo and Sierra Morena of central Spain. Elsewhere in Iberia and Brittany their presence appears to be patchy. *S. salteri salteri* possibly occurs in the Valongo–Arouca region while *C.* cf. *thorali conjugens* is so far only known from Buçaco and Moncorvo in Portugal and probably a similar form is present in the Traveusot Formation, south of Rennes in Brittany (J.-L. Henry pers. comm.). *S. sampelayoi* (Hammann, 1977) has only definitely been recorded in Spain to date.

Early Llandeilo. As in the lower Llanvirn, central Spain appears to have been environmentally homogeneous in that *C. rouaulti*, *S. salteri salteri* and *P. mendax* are known across most of the region, and are also present in eastern Portugal. At Valongo *C. rouaulti* is probably absent although, as indicated above, a poorly preserved ?*Colpocoryphe* may belong to this species. In the Buçaco area the author has not seen specimens of either *S. salteri salteri* or *P. mendax* although Delgado (1908) recorded '*Calymene pulchra*' from the Brejo Fundeiro Formation, Louredo Formation and probably Porto de Santa Anna Formation. In Brittany all three species are known from the median syncline, Domfront and south of Rennes, but *P. mendax* does not occur in the Crozon Peninsula.

The distribution of the above species is informative in terms of environmental differences within the Central Iberian Zone (*sensu* Hammann *et al.* 1982) and Brittany. During early Llanvirn times all the areas appear to show a general similarity in that mud/silt was deposited over a broad shelf



TEXT-FIG. 4. Maps showing distribution of trilobite species during early Llanvirn and early Llandeilo times in Iberia and north-west France. Stippled areas represent outcrop of Ordovician/Silurian rocks.

following the post 'Armorican Quartzite' transgression. Little direct evidence regarding water depth or proximity to shore can be ascertained either from the lithofacies or faunas, and one of the few indications that there was a change in conditions across the Iberian region is seen in the lower diversity of the trilobite faunas from south to north. A similar situation probably existed during early Llandeilo times, although in terms of the species considered here few convincing differences can be seen. However, when consideration is given to a larger sample of the trilobite faunas (Romano 1982), as well as to the lithofacies (Brenchley *et al.* 1986) the differences are considerably more marked. The major contributing factor to the differences in the trilobite assemblages is probably water depth, with its accompanying control on energy level/light/temperature and/or food supply.

It was suggested by Brenchley *et al.* (1986) that the Ordovician shelf in central and western Iberia deepened towards the north in Llandeilo times. This picture fits in well with the observed taphonomy of the trilobite assemblages from Valongo, with their relatively high proportion of complete specimens (Romano 1976) and frequent dispersal within the rock (low energy conditions) compared with the often disarticulated exoskeletons and common bedding plane accumulations at Buçaco (higher energy conditions), particularly above the Monte da Sombadeira Formation.

SYSTEMATIC PALAEONTOLOGY

The classification of *Colpocoryphe* and *Salterocoryphe* has recently been comprehensively discussed by Henry (1980*b*) and Hammann (1983). Henry pointed out reasons for excluding the former from the Homalonotidae (Sdzuy 1957; Bergström 1973; Thomas 1977) and included it, with *Salterocoryphe*, in the Calymenidae. Henry further suggested that *Salterocoryphe* could be placed in the Flexicalymeninae (Siveter 1977), supported by the fact that *Flexicalymene* (*Onnicalymene*) *jemtlandica* and *Salterocoryphe salteri* have almost identical hypostoma, and that *Colpocoryphe* should be restricted to Colpocoryphinae. Hammann (1983), however, favoured the inclusion of both *Salterocoryphe* and *Colpocoryphe* within the Colpocoryphinae of the Calymenidae and considered that *Prionocheilus* of the subfamily Pharostomatinae should be included in the Bathycheilidae.

The suprageneric level of classification is not further discussed here and in the following section the genera are not grouped into higher ranks.

Genus COLPOCORYPHE Novák *in* Perner, 1918

Type species. Calymene arago Rouault, 1849.

Colpocoryphe aff. *rouaulti* Henry, 1970

Plate 1, figs 1–13, 15, 17

?1908 *Calymene Aragoi* Rouault; Delgado, p. 57.
1949 *Synhomalonotus Aragoi* (Rouault); Thadeu, pl. 1, fig. 1.

Material. Two cephala; two cranidia; eight pygidia, with or without attached thoracic segments; thirteen complete, or nearly complete specimens; all preserved as internal and/or external moulds.

Horizon and locality. SG 142 (Thadeu 1949, p. 1, fig. 1), ?143, 500 m N 40° E of Cacemes, Buçaco. SG 144, 450 m S 70° E of Louredo, Buçaco, probably Llanvirn. SG 1326, 100 m N 40° E of Beloi chapel, probably Llanvirn. SG 2190 and MR 59–64, section from Zuvinhal to Santa Ant. do Cantaro, unit 25, Buçaco (Delgado 1908, p. 35), Llanvirn. MR 41, 42, section through Val. San Jorge, unit 20, Buçaco. MR 43–48, same section as specimens 41–42, unit 21, Buçaco (Delgado 1908, p. 42). MR 49–51, Palheiros, Buçaco. MR 52–58, 900 m S 65° E of Venda Nova, Poiares. The material occurs in beds from the Brejo Fundeiro Formation (Llanvirn) to the Fonte da Horta Formation (Llandeilo). MR 41–48 are of Llandeilo age, MR 49–58 are Llanvirn.

Discussion. The material is certainly very close to *C. rouaulti* but differs from it in several respects. In the Portuguese specimens the glabella converges forwards more markedly and the straight anterior margin of the glabella is shorter. The swollen posterior lobe to the central body of the hypostoma is more like that figured by Hammann (1983) while the internal posterior notch is closer to that of Henry's (1970, 1980*a*, *b*) material. The pygidium shows slight differences in the shallower axial and vincular furrows and smaller side lobes. At this stage the author prefers to identify the Portuguese material as *C.* aff. *rouaulti*. Further, the Portuguese material suggests that there may be slight differences between the Llanvirn and Llandeilo forms assigned here to *C.* aff. *rouaulti*. Although the cephala are virtually indistinguishable the pygidial axis of the stratigraphically lower specimens tends to carry less well-defined ring furrows and the vincular furrows are less strongly indented than in the Llandeilo forms. It is possible that the Llanvirn material may prove to be subspecifically distinct from the Llandeilo form, but this must await more and better preserved material.

Colpocoryphe cf. *thorali conjugens* Hammann, 1983

1986 *Colpocoryphe* cf. *thorali conjugens* Hammann; Romano *et al.*, p. 429, pl. 1, figs 2–5.
1988 *Colpocoryphe* cf. *thorali conjugens* Hammann; Rebelo and Romano, p. 54, pl. 1, figs 8–11; pl. 2, fig. 5.

Material. Four cranidia; two cranidia, with part thorax; three pygidia; all preserved as internal and/or external moulds.

Horizon and locality. P157/7, 1·2 m above lingulid bed at top of Armorican Quartzite Formation, road section south of River Mondego, Penacova. RC1/2, 10 cm above lingulid bed at top of Armorican Quartzite Formation, track section, north of River Ceira, Vila Nova do Ceira. SG 1154/1–4, 6, 10, Xistenta Formation, 3·5 km ESE of Mos, 13 km east of Moncorvo. P157/7 and RC1/2 are Lower Llanvirn, SG 1154/1–4, 6, 10, probably Llanvirn.

Discussion. For description and discussion of the above material see Romano *et al.* (1986) and Rebelo and Romano (1988). Nothing new can be added. The subspecies is known from lower Llanvirn of the Sierra Morena (Hammann 1983; Rábano 1984; Gutiérrez-Marco *et al.* 1984).

Colpocoryphe grandis (Šnajdr, 1956)

Plate 2, figs 1–3, 7, 8, 11

?1908 *Calymene Aragoi* Rouault; Delgado, pp. 41, 57.
*1956 *Calymene* (*Colpocoryphe*) *grandis* Šnajdr; p. 529, pl. 3, figs. 1–9.
1980*b* *Colpocoryphe grandis* (Šnajdr, 1956); Henry, text-fig. 3, pl. 2, figs 3 and 4.

(for full synonymy see Henry 1980*a*, p. 64; and Hammann 1983, p. 85).

Material. Three cephala; three cranidia; two cephala, with part of thorax; five pygidia, with part of thorax; two pygidia; two complete or nearly complete specimens; all preserved as internal and/or external moulds.

Horizon and locality. LOR 1.007–9, Louredo Formation, Favaçal Bed, Louredo village. LOR 2.001, less than 2 m below Favaçal Bed, Louredo village. PEN 1.001–2, less than 10 m below Favaçal Bed, quarry 320 m ENE

EXPLANATION OF PLATE 1

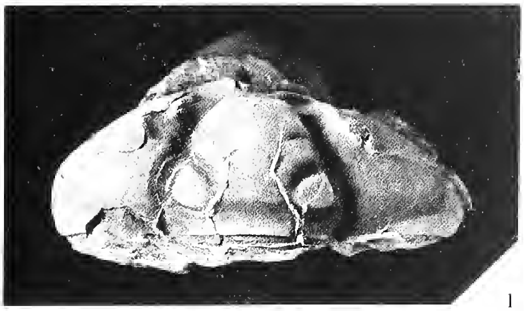
Figs 1–13, 15, 17. *Colpocoryphe* aff. *rouaulti* Henry, 1970. 1–3, SG 142; internal mould of cephalon, dorsal, anterior and lateral views, ×2, Brejo Fundeiro Formation, Buçaco, Llanvirn. 4, MR 41; internal mould of cranidium, dorsal view, ×1·4, Fonde da Horta Formation, Buçaco, Llandeilo. 5, MR 42; internal mould of cranidium, dorsal view, ×2, Fonte da Horta Formation, Buçaco, Llandeilo. 6–8, MR 52; internal mould of cranidium, dorsal, anterior and lateral views, ×1·8, Brejo Fundeiro Formation, Poiares, Llanvirn. 9, MR 44; internal mould of cranidium, dorsal view, ×1, ?Fonte da Horta Formation, Buçaco, Llandeilo. 10, SG 144; internal mould of pygidium, dorsal view, ×2, Brejo Fundeiro Formation, Buçaco, ?Llanvirn. 11, SG ?143; internal mould of pygidium, dorsal view, ×2, Brejo Fundeiro Formation, Buçaco, ?Llanvirn. 12, MR 49; internal mould of pygidium, dorsal view, ×2, Brejo Fundeiro Formation, Buçaco, Llanvirn. 13, MR 53; internal mould of pygidium, dorsal view, ×2, Brejo Fundeiro Formation, Poaires, Llanvirn. 15, MR 46; internal mould of nearly complete specimen, dorsal view, ×1, ?Fonte da Horta Formation, Buçaco, Llandeilo. 17, MR 45; internal mould of nearly complete specimen, ×1, ?Fonte da Horta Formation, Buçaco, Llandeilo.

Fig. 14. *Colpocoryphe* sp. MD 2.001/2; internal mould of incomplete cranidium, dorsal view, ×6, Carregueira Formation, Dornes, Caradoc.

Fig. 16. *Colpocoryphe*? sp. indet. SG 146; partly enrolled specimen with 6 thoracic segments and pygidium, dorsal view of pygidium, ×1.2, Fonte da Horta Formation, Buçaco, Llandeilo.

Fig. 18. *Salterocoryphe salteri salteri* (Rouault, 1851). SG 1681; internal mould of pygidium, dorsal view, ×0·9, Valongo Formation, Valongo, Llandeilo.

PLATE 1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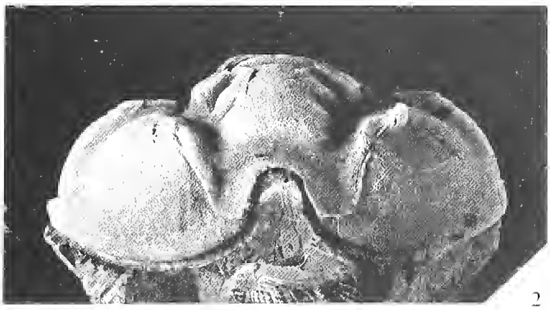
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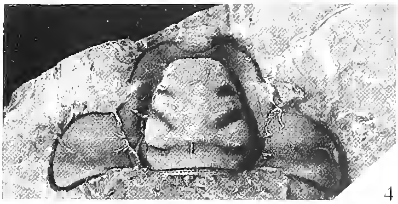
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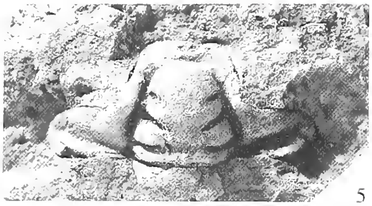
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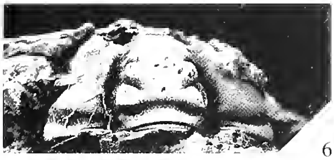
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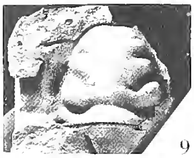
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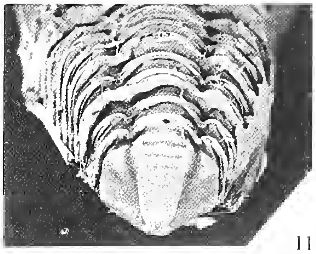
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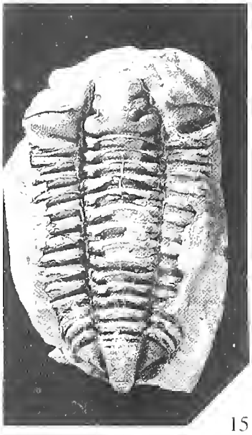
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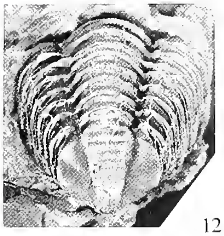
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ROMANO, *Colpocoryphe*, *Colpocoryphe*?, *Salterocoryphe* of east end of bridge over River Mondego, east of Penacova. QXP 2.001–5, 40, and Mação specimen of Cooper (1980), '1700 m N 57° E de pyr. de Queixoperra, Mação', probably from 'Bryozoa Beds' (Cooper 1980; Romano 1982) within unit 7 of the 'Schistes à *Orthis Berthoisi*' (Delgado 1908, p. 92), Queixoperra Member of Cabeço do Peão Formation. CST 2.001–4, 1400 m N 62° E of Pereiro, Mação, oolitic beds probably equivalent to basal oolite (Favaçal Bed) of Louredo Formation. ABO 9.001, Aboboreira, Carregueira Formation, from less than 3 m below oolitic beds, and ABO 10.001, basal 'Bryozoa Beds', Queixoperra Member, both approximately 1 km WNW of Carregueira, Mação. T. Young collection, unnumbered specimens from 2 km SSE of Aboboreira [20710, 28915], and west of Pereiro [20975, 29090]; all from Favaçal Bed. Dornes material (loc. 70), grid reference 18992 31368, from 'Bryozoa Beds' of Cabeço do Peão Formation. Fragmental material is also known from near the top of the Carregueira Formation at Rio Ceira (Young 1985). All specimens are probably of early Caradoc age.

Discussion. The present material agrees in all important respects with that described and figured by Snajdr (1956), Destombes (1966), Henry (1980*a*) and Hammann (1983).

Colpocoryphe? sp. indet.

Plate 1, fig. 16

?1908 *Calymene transiens* Verneuil and Barrande; Delgado, p. 57.
1949 *Synhomalonotus transiens* (Verneuil and Barrande); Thadeu, pl. 1, fig. 6.

Material. SG146. Internal mould of enrolled specimen with six thoracic segments and pygidium (Thadeu 1949, pl. 1, fig. 6).

Horizon and locality. '100 m S 80° E of Loredo', Buçaco. Delgado (1908, p. 57) records the species from the 'Schistes à *Homalonotus oehlerti*' (Fonte da Horta Formation) of Llandeilo age.

Description. Thoracic segments of *Colpocoryphe* type (see Henry 1980*a*, pl. 7, fig. 1*a*) carrying sculpture of small tubercles. Pygidial axis wide anteriorly, narrowing evenly backwards and with shallow axial furrows, posterior part not preserved. Eight visible axial rings seen separated by shallow, complete ring furrows. Small triangular pleural lobes extend back to eighth axial ring and carry up to four poorly defined ribs. Lateral borders have wide, open furrows with no trace of segmentation on lower surfaces. Sculpture slightly coarser than on thorax.

Discussion. The absence of segmentation on the lateral borders is typical of the genus *Colpocoryphe* as distinct from *Salterocoryphe*. The ribs on the pleural lobes are more obvious than in *C. rouaulti* and *C. grandis* and there is no median shallowing of the axial ring furrows in the pygidium as in the latter species, although this feature is more apparent on external moulds (Henry 1980*a*, pl. 7, figs 6*a*, *b* and 7; pl. 8, fig. 2*a*–*d*).

EXPLANATION OF PLATE 2

Figs 1–3, 7, 8, 11. *Colpocoryphe grandis* (Šnajdr, 1956). 1, QXP 2.0001; internal mould of incomplete cranidium, dorsal view, ×1, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 2, 7, QXP 2.040; internal mould of pygidium, dorsal and posterior views, ×1 and ×1·4 respectively, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 3, PEN 1.002; internal mould of pygidium, dorsal view, ×1, Carregueira Formation, Amêndoa/Mação, Caradoc. 8, CST 2.004; internal mould of cephalon, anterior view, ×0·6, Favaçal Bed, Mação, Caradoc. 11, CST 2.003; internal mould of fragmentary cephalon and hypostoma, anterior view, ×0·7, Favaçal Bed, Mação, Caradoc.

Figs 4–6, 9, 10, 12. *Salterocoryphe salteri salteri* (Rouault, 1851). 4, SG 1687.1; internal mould of incomplete specimen, dorsal view, ×1, Valongo Formation, Valongo, Llandeilo. 5, SG 149; internal mould of complete specimen, dorsal view, ×1·3, Valongo Formation, Valongo, Llandeilo. 6, SG 1686.1; internal mould of partly enrolled specimen, dorsal view, ×1·2, Valongo Formation, Valongo, Llandeilo. 9, SG 1325; internal mould of specimen with hypostoma, dorsal view, ×1·4, Valongo Formation, Valongo, Llandeilo. 10, 12, SG 1687; internal mould of nearly complete specimen, dorsal view, ×1, anterior view, ×1·4, respectively, Valongo Formation, Valongo, Llandeilo.

PLATE 2


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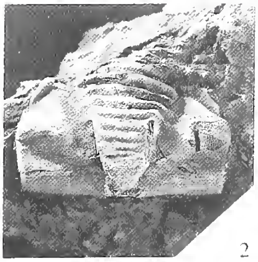
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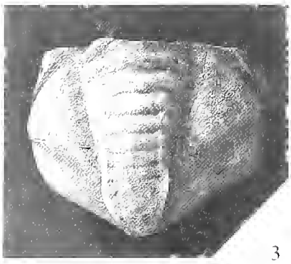
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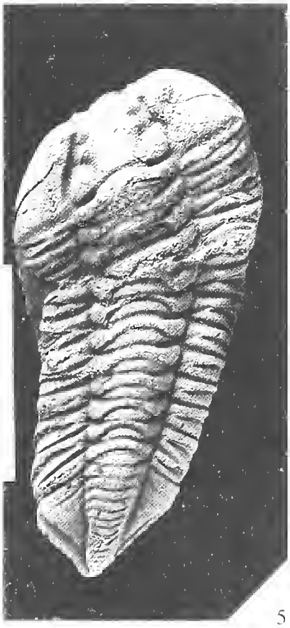
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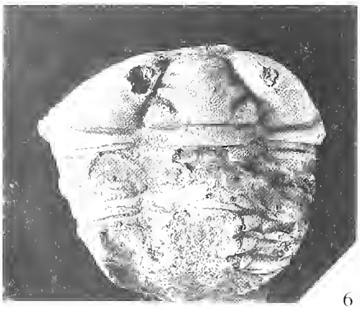
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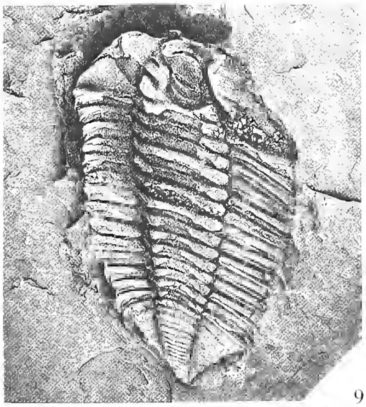
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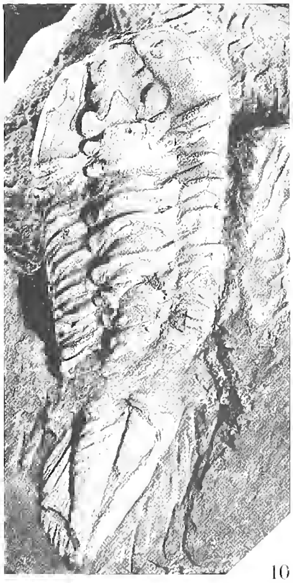
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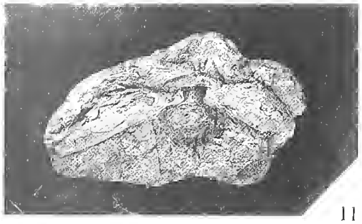
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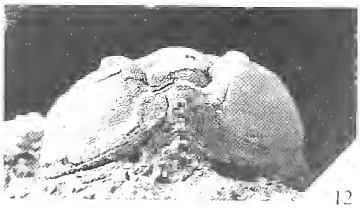
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ROMANO, *Colpocoryphe*, *Salterocoryphe*

The incomplete specimen precludes specific identification. Delgado and Thadeu referred the species to '*Calymene transiens*' (Verneuil and Barrande 1855, p. 974, pl. 25, fig. 5) from Almadén, Spain, but Verneuil and Barrande's figure and description do not permit a close comparison. Tromelin and Lebesconte (1876, p. 629) reinvestigated the type of *transiens* and regarded it as belonging to '*Calymene salteri*'. Henry (1970, p. 22) pointed out that *Salterocoryphe salteri* is present at Almadén which tends to support Tromelin and Lebesconte's suggestion.

Hammann (1983, p. 90) reported that the type of *Calymene transiens* could not be found and that the species cannot reliably be attributed to either *Colpocoryphe* or *Salterocoryphe*. However, Hammann considered it to be closer to the latter.

Colpocoryphe sp.

Plate 1, fig. 14

Material. MDC 2.001/2, part and counterpart of incomplete cranidium.

Horizon and locality. Carregueira Formation, Dornes, type section (Young 1985), about 5 m below oolitic horizon (at base of Cabeço do Peão Formation). Lower Caradoc.

Description. Glabella (excluding occipital ring) slightly longer than wide, sides gently converging anteriorly. Occipital furrow forwardly flexed, occipital ring carries small median tubercle which is considerably fainter on external mould. Anterior margin of glabella gently rounded with short, straight median part. S2 furrows are short, straight and inclined only slightly backwards; S3 very short and indistinct. Anterior notch of cranidium is broad with widely diverging sides. Cranidium is finely tuberculate.

Discussion. The specimen is small (about 4·5 mm long) and may represent a meraspid stage. The open anterior notch suggests affinities with *Colpocoryphe grandis* but this species does not possess such a narrow glabella, at least in adult specimens, or a median occipital tubercle. The short S2 and S3 furrows and fine sculpture are features of *Salterocoryphe salteri salteri* (Hammann 1977; Henry 1980*a*) and the juvenile of this species bears a median occipital tubercle (Hamman 1983, pl. 11, fig. 110). However the structure of the anterior cephalic border is typical of *Colpocoryphe* and until juvenile specimens of *C. grandis* are described it is preferable to leave the Portuguese specimen in open nomenclature.

Genus SALTEROCORYPHE Hamman, 1977

Type species. Calymene salteri Rouault, 1851.

Salterocoryphe salteri salteri (Rouault, 1851)

Plate 1, fig. 18; Plate 2, figs 4–6, 9, 10, 12; Plate 3, fig. 9.

*1851 *Calymene salteri* Rouault, p. 358.
1949 *Synhomalonotus salteri* (Rouault) Thadeu, pl. 1, figs 2–3.
1949 *Synhomalonotus lusitanica* Delgado; Thadeu, p. 131, pl. 1, figs 7–9; pl. 2, figs 1 and 2.
1960 *Neseuretus lusitanica* (Thadeu); Whittard, p. 145.
1966 *Colpocoryphe lusitanica* (Thadeu); Dean, p. 309.
1982 *Neseuretus lusitanicus* (Thadeu); Fortey and Morris, p. 70.
1982 *Salterocoryphe lusitanica* Romano, p. 96.
1982 *Salterocoryphe salteri* Romano *in* Hammann, Robardet and Romano, p. 40.

(for full synonymy see Henry 1970, p. 18; and Hammann 1983, p. 90).

Material. Five complete or nearly complete specimens; fourteen other specimens; all preserved as internal or external moulds.

Horizon and locality. SG 147 (figured by Thadeu 1949, pl. 2, fig. 2), 'vizinhanças de Valongo'. SG 148 (Thadeu 1949, pl. 1, fig. 9), '800 m NE de Boloi'. SG 149 and 150 (Thadeu 1949, pl. 1, figs 7 and 8), 'Ribeira da Murta, Valongo'. SG 1688, (Thadeu 1949, pl. 2, fig. 1) '1650 m (non 1680 m, Thadeu 1949, p. 131) S 20° W da piramide de Santa Justa'. SG 1323 and 1324, '1000 m S 30° E da igreja de Covelo, Valongo'. Information taken from labels on specimens, slightly modified using Thadeu (1949). Other specimens from Beloi, Covelo, Santa Justa and Penha Garcia (see Text-fig. 1). PG 6.001 from approximately 11 m above Monte da Sombadeira Formation, Penha Garcia. All north Portuguese material is probably from upper part of the Valongo Formation (Schistes à *Uralichas Ribeiroi* of Delgado 1908) of Llandeilo age.

Discussion. The species has been recently described and figured by Henry (1970) and Hammann (1983). Henry (1980*a*) distinguished two subspecies of *S. salteri* of which the Portuguese material may be assigned to *S. salteri salteri*.

Since Thadeu (1949) first described *Salterocoryphe lusitanica*, various authors (Whittard 1960; Dean 1966) have briefly referred to it in discussions relating to generic assignment. Henry (1970, p. 21) discussed the status of the species when he suggested that it bore a striking resemblance to *S. salteri* in that the form of the glabella, eye position and number of axial rings were identical. The only difference that Henry noted was that the pleural lobes on the pygidium were more clearly segmented in the Portuguese material, but this he thought could well be the result of deformation. A study of additional material indeed confirms Henry's suggestion that the preservation of the furrows varies with the deformation. The anterior part of the pygidial axis tends to be relatively narrower in the Portuguese specimens but this does not seem to be an important criterion for separating the two forms. Hence I prefer to put *lusitanica* into synonymy with *salteri*. Hammann (1983, p. 93) regarded *lusitanica* as a distinct species but his criteria are not accepted here; for example the range in glabella length: width ratios of *salteri* and *lusitanica* are virtually identical and the ornament of specimens assigned to *lusitanica* is similar to that of *salteri*.

Genus PRIONOCHEILUS Rouault, 1847

(Syn. *Pharostoma* Hawle and Corda, 1847)

Type species. *Prionocheilus verneuili* Rouault, 1847.

Remarks. The question of the priority of *Prionocheilus* Rouault, 1847 or *Pharostoma* Hawle and Corda, 1847 has been discussed by Dean (1964, 1966, p. 300; 1971, p. 42), Whittington (1965, p. 56), Ingham (1977, p. 103), Siveter (1977, pp. 339, 393), Owen and Bruton (1980, p. 2), Henry (1980*a*, p. 79) and Hammann (1983, p. 51). For the present paper I prefer to accept Dean's argument and follow his suggestion for using *Prionocheilus*.

Prionocheilus mendax (Vaněk, 1965)

Plate 3, figs 1–5, 8

1908 *Calymene pulchra* Barrande; Delgado, pp. 106, 134, ?138.
1942 *Calymene pulchra* Barrande; Costa, p. 93.
1949 *Calymene pulchra* Barrande; Thadeu, p. 129, pl. 2, figs 3–5.
*1965 *Pharostoma pulchrum mendax*; Vanek, pp. 30–32, fig. 6; pl. 2, fig. 10; pl. 3, figs 6 and 7; pl. 4, figs 2–5.

(for a full synonymy see Vaněk 1965, p. 30; Henry 1980*a*, pp. 80–81; and Hammann 1983, p. 53).

Material. Three cephala with part thorax; one hypostoma; two free cheeks; twenty-three complete or nearly complete specimens; all preserved as internal and/or external moulds.

Horizon and locality. SG 151, 'Valongo'. SG 1692, 1692.1–3, 1693.1 and MR 38–40, 1400 m S 32° E of Covelo church, Valongo. SG 1327, 1327.1, 1000 m S 30° E of Covelo church, Valongo. SG 1691, 1691.1–3, 800 m S 26° W of 'ermida de Santa Justa, Valongo'. Delgado (1908) records the species from the 'Schistes à *Didymograptus*' (Llanvirn) to the 'Schistes à *Uralichas Ribeiroi*' (Llandeilo) of the Valongo Formation

(Romano and Diggens 1976; it is not possible to relate his specimens to exact horizons. The author has collected this species from beds of Llandeilo age at Valongo but has not recorded it from the Llanvirn.

Description. A full description is not given since the species is well documented. Cephalon semicircular in outline with evenly rounded anterior and lateral margins. Glabella subtriangular in outline, with evenly curved anterior margin and slightly curved sides. Maximum width of cephalon about two and a half times that of posterior glabellar width. Glabella from 0.7–0.8 times as long as cephalon. Three pairs of glabellar lobes and furrows. Faint oval areas situated on inner side of posterior branch of 1S. Glabella gently convex dorsally. Axial furrows generally deep, expanding into small, crescent-shaped paraglabellar areas abaxial to 1L. Palpebral lobes prominent, situated opposite 2L and nearer to axial furrow than lateral margin. Faint eye ridge runs to 2S. Free cheeks with long, posteriorly directed genal spines. Lateral and anterior margin of cephalon carry at least fifty downwardly directed, slightly curved (posteriorly) spines. Sculpture of small tubercles of uniform size, absent in paraglabellar areas.

Hypostoma consists of gently convex, subovate middle body, longer than wide, with shallow inwardly directed furrows defining a posterior crescent-shaped lobe; lobe consists of two oblique lateral lobes. Anterolateral margins with small outwardly directed pointed wings. Posterior margin of hypostoma has a shallow open notch; posterior projections are rounded.

Thorax consists of thirteen segments. Axial furrows gently outwardly curved; axis widest at about third axial ring where it is over one and a half times as wide as at posterior end. Axial rings lobate laterally. Broad (trans.), horizontal inner parts of pleural region, outer parts bent sharply down. Pleural furrows deep, wide (exsag.) and straight, starting at anterolateral corner of axial ring and running approximately parallel to pleural margins. Posterior border slightly wider (exsag.) than anterior. At geniculation, furrows swing forwards and die out before reaching rounded tip of segment. Thorax finely tuberculate like cephalon.

Pygidium semicircular in outline. Anterior end of axis about one-third maximum width of pygidium. Axis narrows evenly backwards, not reaching posterior margin. Axis carries five rings (sometimes with faint suggestion of a sixth) and a semicircular terminal piece which stands higher than rest of axis. Ring furrows shallow and narrow (sag.) posteriorly. Up to five nearly straight ribs, separated by deep furrows which curve strongly backwards distally. First, three/four ribs carry short furrows extending from axial furrow. Sculpture similar to that of cephalon and thorax.

EXPLANATION OF PLATE 3

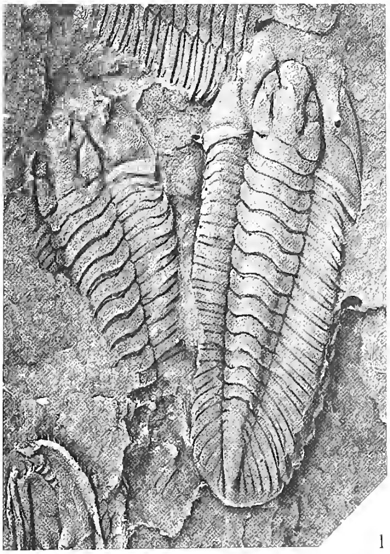
Figs 1–5, 8. *Prionocheilus mendax* (Vaněk, 1965). 1, MR 38.3 and 38.5; latex cast of external mould, dorsal view, × 1, Valongo Formation, Valongo, Llandeilo. 2, MR 38.6–8; latex cast of external mould, dorsal view, × 0·8, Valongo Formation, Valongo, Llandeilo. 3, MR 39; internal mould of incomplete specimen, dorsal view, × 1, Valongo Formation, Valongo, Llandeilo. 4, MR 38.1; latex cast of external mould, dorsal view, × 1, Valongo Formation, Valongo, Llandeilo. 5, SG 1692.1; latex cast of internal mould showing hypostoma, dorsal view, × 1, Valongo Formation, Valongo, Llandeilo. 8, MR 38.13; latex cast of external mould of free cheek, dorsal view, × 1, Valongo Formation, Valongo, Llandeilo.

Figs 6, 10, 12, 13. *Prionocheilus* cf. *pulcher* (Barrande, 1846). 6, QXP 2.017; latex cast of external mould of cranidium, dorsal view, × 3, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 10, SG 152; internal mould of cranidium, dorsal view, × 1·5, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 12, QXP 2.014; internal mould of cranidium, dorsal view, × 2, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 13, QXP 2.009; latex cast of external mould of pygidium, dorsal view, × 2, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc.

Fig. 9. *Salterocoryphe salteri salteri* (Rouault, 1851). PC 6.001; latex cast of external mould of cranidium, dorsal view, × 1·75, Fonte da Horta Formation, Penha Garcia, Llandeilo.

Figs 7, 11, 14–16. *Actinopeltis tejoensis* sp. nov. 7, QXP 2.041; internal mould of pygidium, dorsal view, × 2, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 11, QXP 2.043; internal mould of incomplete pygidium, dorsal view, × 3, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 14, QXP 2.006; internal mould of cephalon, dorsal view, × 2, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc. 15 and 16, SG 225 (holotype); internal mould and latex cast of corresponding external mould, dorsal views, × 1·4 and 1·8 respectively, Cabeço do Peão Formation, Amêndoa/Mação, Caradoc.

PLATE 3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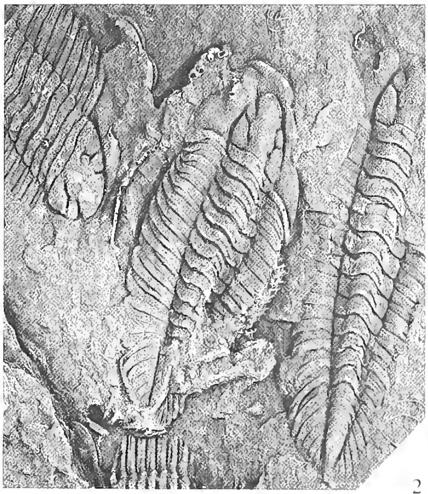
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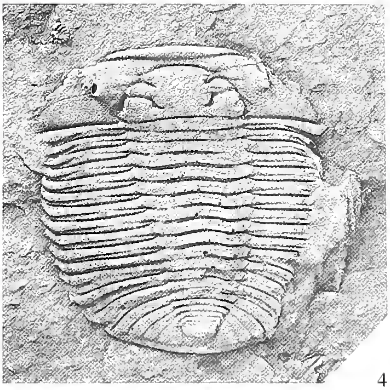
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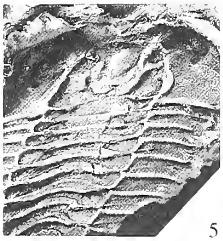
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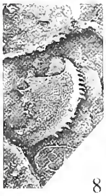
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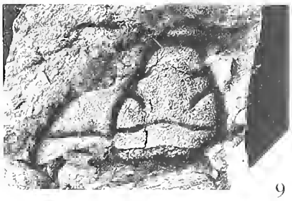
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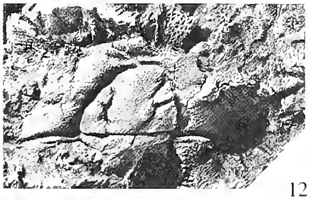
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ROMANO, *Prionocheilus*, *Salterocoryphe*, *Actinopeltis*

Discussion. The Portuguese material is very similar to that figured by Vaněk (1965) from the Dobrotivá Formation (Llandeilo) to Letná Formation (lower Caradoc) of Bohemia. A minor difference is the shallower posterior axial ring furrows and pleural furrows. This was also noted by Henry (1980*a*, p. 81) who recorded the species from the upper part of the Traveusot and Andouillé formations (Llandeilo) of Brittany. Henry (1980*a*) figured an *in situ* hypostoma and commented on the difference between it and that figured by Vaněk (1965, pl. 2, fig. 10). Vaněk's specimen of a hypostoma is incomplete and contrasts with the notched posterior margin of specimens from Brittany (Henry 1980*a*, fig. 31, pl. 14, fig. 3*a*) and Spain (Hammann 1983, text-fig. 14). Although the two Portuguese *in situ* hypostomata are not well-preserved, they both show the notched posterior margin; the posterior projections, however, have more rounded outlines than in the Brittany specimen. The minor differences mentioned above are considered insufficient to separate the Portuguese species from *Prionocheilus mendax*.

Prionocheilus cf. *pulcher* (Barrande, 1846)

Plate 3, figs 6, 10, 12, 13

1908 *Calymene pulchra* Barrande; Delgado, pp. 57, 80.

Material. Thirteen cranidia; one free cheek; two cephala with part of thorax; four pygidia; all preserved as internal and/or external moulds.

Horizon and locality. SG 152, 'Aboboreira, 300 m N 60° W (Mação)', from the 'Schistes à *Orthis* (= *Svobodaina*) *Berthoisi*' (Delgado 1908, p. 80, but not listed in following descriptions of stratigraphic sections). QXP. 2.008–2.028, '1700 m N 57° E de pyr. de Queixoperra', Mação; 'Bryozoa Beds', Queixoperra Member, 'Schistes à *Orthis Berthoisi*'. ABO 10.002, approximately 1 km WNW of Carregueira, Mação; basal 'Bryozoa Beds', Queixoperra Member, Cabeço do Peão Formation. All material of Caradoc age (probably early).

Description. Glabella subtriangular in outline with nearly straight anterior margin, length just over three-quarters the basal width. Glabella nearly two-thirds as long as cranidium. Occipital ring about same length as anterior border medially. Behind L1, occipital ring is constricted and swings forwards where at posterolateral corner of L1 it is half of its median length. Occipital furrow shallow and straight behind central glabellar lobe; at inner posterior corner of L1 furrow deepens and remains so to axial furrow. Three pairs of unequal glabellar lobes. L1 largest, length just under half that of glabella, with nearly straight lateral and posterior margin, and angular anterolaterally. S1 shallow near axial furrow, deepest at inner anterior corner of L1 where furrow bifurcates. Posterior branch runs backwards and curves inwards; anterior branch shallow and short, directed inwards and forwards. L2 just over half the length of L1, with more or less straight anterior and posterior margins. S2 straight, shallow near axial furrow, directed inwards and backwards at a smaller angle to the midline than S1. L1 and L2 separated from central glabellar lobe by very faint furrow. L3 very small and delimited anteriorly by very faint S3. Oval areas situated adaxial to posterior branch of S1. Glabella gently convex (trans. and sag.). Axial furrow gently curved, convex outwards, shallowest opposite L2 and at posterior end of L1. Outside L1, axial furrow expanded into crescent-shaped paraglabellar areas. Anterior pit associated with slightly inwardly placed large tubercle situated on outer side of axial furrow, just anterior to S3. Preglabellar field separated from glabella by narrow, shallow furrow; preglabellar field of same length as anterior border and slopes gently backwards. Prominent, convex (sag.) anterior border separated from preglabellar field by well marked furrow which shallows abaxially. Posterior border narrow (exsag.) at axial furrow, widening abaxially. Back of palpebral lobe level with where S1 meets axial furrow, anterior margin of palpebral lobe approximately level with anterior corner of L2. Palpebral lobe slopes inwards and merges with fixed cheek. Faint eye ridge running inwards and forwards from palpebral lobe to meet axial furrow just behind anterior pit. Anterior branch of facial suture runs in slightly sigmoidal curve to cut anterior margin in-line approximately with outer part of paraglabellar areas (preservation poor). Posterior branch of facial suture runs outwards and backwards (posterolateral parts of fixed cheeks not preserved). Free cheek narrow, extending into long, posteriorly directed genal spine reaching back to at least 6th thoracic segment. At least nineteen ventrally directed and slightly curved spines (just under 0·5 mm long) situated along border. Sculpture on cephalon of fine tubercles, about twenty per square mm; absent in furrows and very sparse on preglabellar field.

Hypostoma not known. Thorax of *Prionocheilus* type, tuberculate except in furrows. Pygidium strongly curved anteriorly, gently curved posterior margin. Pygidium two and a half times as wide as anterior part of axis; latter narrows evenly posteriorly and about four-fifths length of pygidium. Seven axial rings narrowing (sag.) posteriorly, 6th and 7th axial ring furrows weak to absent medianly. Terminal piece about one-quarter axial length, broadly rounded and sloping down steeply posteriorly. Six pairs of ribs separated by deep furrow which terminate just before lateral margins. Surface of pygidium tuberculate.

Discussion. In most features the Mação specimens are very close to *Prionocheilus pulcher* (Barrande 1852, pl. 19, figs 1–3, 6; see also Vaněk 1965, p. 31, pl. 3, figs 3–5, pl. 4, fig. 1, text-fig. 5). Minor differences include the straighter anterior border in the Portuguese specimens and the less dense ornament, particularly on the fixed cheeks (cf. Vaněk 1965, pl. 3, fig. 4). *P. pulcher* is known from the Vinice, Zahořany and Bohdalec Formations of Bohemia (Havlíček and Vaněk 1966) but is only tentatively recorded from NW France (Henry 1980*a*, p. 187) where, however, the very similar *P. verneuili* Rouault is known from beds of Caradoc age to the south of Rennes (Riadan Formation) and possibly in the Crozon Peninsula (top of Postolonnec Formation) (Henry 1980*a*, p. 80). Henry stated, as Dean (1966, p. 303) had noticed, that the deformation of the Riadan specimens made some of the distinguishing features less certain; thus the status of *verneuili* is still in doubt.

Prionocheilus costai (Thadeu, 1947)

Plate 4, figs 1–9

- 1908 *Calymene Costai* Delgado, p. 57.
- *1947 *Pharostoma Costai* (Delgado); Thadeu, p. 218, pl. 2, figs 5–10.
- 1949 *Pharostoma Costai* (Delgado); Thadeu, p. 130.
- 1960 *Pharostoma Costai* (Delgado); Whittard, p. 138.
- 1976 *Prionocheilus costai* (Delgado); Hammann, p. 39, pl. 4, figs 46–51; pl. 5, figs 52–58; text-fig. 7.
- 1980*a* *Prionocheilus costai* (Delgado); Henry, p. 80.
- 1982 *Prionocheilus costai*; Hammann *et al.*, p. 23.
- 1983 *Prionocheilus costai* (Delgado 1908); Hammann, p. 55, pl. 3, figs 34–36.
- 1984 *Prionocheilus costai* (Delgado); Rábano, p. 272.

Material. Designated lectotype: SG 160 (Thadeu 1947, pl. 2, fig. 8). Paralectotypes: SG 161–163 (Thadeu 1947, pl. 2, figs 7, 5 and 6 respectively). Three cephala with part of thorax; two nearly complete specimens; all preserved as internal and/or external moulds.

Horizon and locality. All specimens are listed by Delgado (1908) as occurring in the 'Schistes culminants et schistes diabasiques', 250–300 m N 40° W of Louredo. Porto de Santa Anna Formation, late Caradoc-Ashgill age. The specimens are probably from the lower part of the unit, the Leira Ma Member.

Description. Since the species has already been described by Thadeu (1947) and a further full account was given by Hammann (1976), only additional notes will be given here.

Thadeu noted that only two pairs of glabellar furrows are present. However, on specimens SG 160 and 161, short, shallow inwardly directed S3 start level from where the eye ridge meets the axial furrow. The L3 thus defined are very short (exsag.) and less than half the length of L2. Over sixty downwardly directed short spines are present on the convex cephalic doublure and are continuous around the anterior margin of the cephalon. The axial rings and posterior and anterior bands on the pleurae carry numerous large tubercles. On specimen SG 162 these tubercles are seen to form the bases of short posterodorsally directed spines up to 0·5 mm in length. The pygidium is nearly three times as wide as long. The axis consists of five rings and a terminal piece, and four (five) backwardly directed pleural furrows with less distinct interpleural furrows.

Discussion. Delgado first used the specific name *costai* in a faunal list (1908, p. 57). Although he did not describe or figure the species, later authors (see synonymy above) have credited it to Delgado, following the practice of Thadeu (1947) who was the first to formally describe the species. In this work authorship is attributed to Thadeu.

All the differences between *P. costai* and *P. pulcher* (Barrande) (authorship attributed to Beyrich by Whittard 1960, p. 134) listed by Whittard (1960, p. 138) are now known not to be valid. Thus *P. costai* does possess a spinose cephalic border and preglabellar field (although in Hammann 1976, text-fig. 7 the spines do not appear to be continuous around the anterior margin). Also the glabella has straighter sides in the Iberian species, there are fewer pygidial ribs and the granular sculpture is coarser.

Genus ACTINOPELTIS Hawle and Corda, 1847

Type species. Actinopeltis globosa (Barrande, 1852).

Actinopeltis tejoensis sp. nov.

Plate 3, figs 7, 11, 14–16; Text-fig. 5

1908 *Cheirurus* sp. n.; Delgado, p. 80.

Diagnosis. Species of *Actinopeltis* with the following characteristics: large, inflated, spherical anterior part of glabella; small isolated basal glabellar lobes separated from inflated glabellar lobe by long (*sag.*) furrow. Eyes situated far back, with eye ridge running to just anterior of S2. Pygidium with four pairs of spinose pleurae; posterior pair short to nearly as long as third pair.

Type material. Holotype: SG 225, part and counterpart of nearly complete individual. Paratypes: QXP 2.006, 2.007, 2.026, internal moulds of incomplete cephala. QXP 2.041/2, 2.043/4, parts and counterparts of pygidia.

Horizon and locality. SG 225 from '500 m N 52° E do logar do Pereiro (Mação)'. Other specimens from '1700 m N 57° E de pyr. de Queixoperra', Mação. All specimens from 'Schistes à *Orthis Berthoisi*' (Delgado 1908, p. 80), Queixoperra Member of the Cabeço do Peão Formation, of Caradoc age.

Derivation of name. From the Portuguese name Rio Tejo (River Tagus), into which drain the rivers of the Mação area.

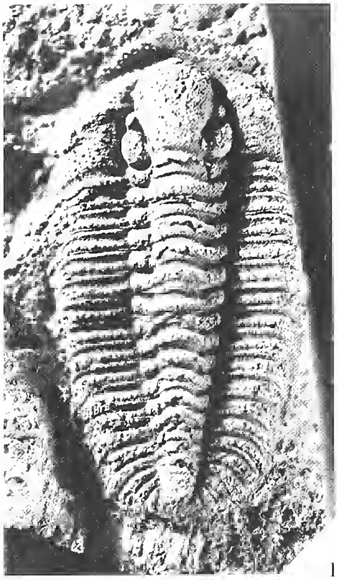
Description. The total length of specimen SG 225 is 28 mm of which the cephalon constitutes nearly 8 mm and the thorax about 12 mm. The specimen is obliquely deformed and crushed; the right side has been damaged.

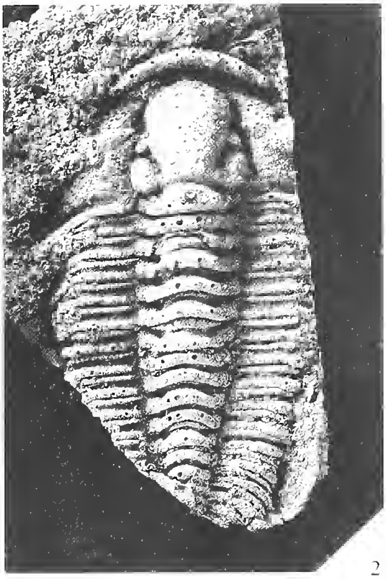
Cephalon dominated by large, approximately spherical anterior part of glabella, which is slightly wider than long and covered with small, closely spaced tubercles (barely visible on internal mould). Narrow (trans.) posterior part of glabella (though varies with preservation) comprises pair of small, nodular basal lobes, anterior to which a broad furrow separates them from inflated anterior part of glabella. Occipital furrow indistinct, merging with transverse furrow anterior to L1 which are thus isolated at abaxial portions of broad (sag.) furrow. Occipital ring convex (sag. and trans.) and carrying similar ornament to glabella. Faint, shallow S2 start just posterior to where eye ridge meets axial furrow; S2 possibly directed slightly forwards but fracturing of glabella makes this uncertain. Short, shallow S3 situated approximately level to where lateral border furrow meets axial furrow. Axial furrows deep, without sculpture, and widely divergent.

Cheeks small, triangular in outline, highest part lying adjacent to basal glabellar lobes. Lateral border strongly convex, of more or less constant width, extending with posterior border into long genal spine back to at least seventh thoracic segment. Genal spine oval(?) in cross-section and covered with small, densely

EXPLANATION OF PLATE 4

Figs 1–9. *Prionocheilus costai* (Thadeu, 1947). 1–3, SG 160 (designated lectotype); internal mould and latex cast of external mould of nearly complete specimen, dorsal and anterodorsal views, ×2·7, ×3 and ×3 respectively, Porto de Santa Anna Formation, Buçaco, Caradoc/Ashgill. 4, SG 2849; latex cast of external mould of incomplete cephalon and thorax, dorsal view, ×3, Porto de Santa Anna Formation, Buçaco, Caradoc/Ashgill. 5, SG 162; internal mould of cephalon and part thorax, dorsal view, ×3, Porto de Santa Anna Formation, Buçaco, Caradoc/Ashgill. 6, 9, SG 161; latex cast of external mould and internal mould of incomplete specimen, dorsal views, ×2·4, Porto de Santa Anna Formation, Buçaco, Caradoc/Ashgill. 7 and 8, SG 163; internal mould and latex cast of external mould of nearly complete specimen, dorsal views, ×3 and ×3·4 respectively, Porto de Santa Anna Formation, Buçaco, Caradoc/Ashgill.


1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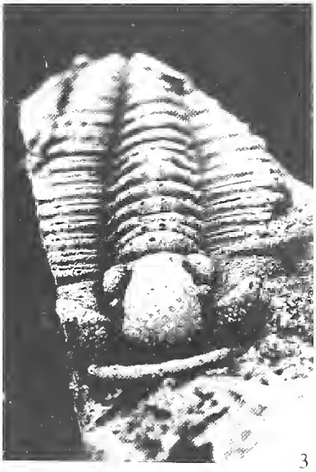
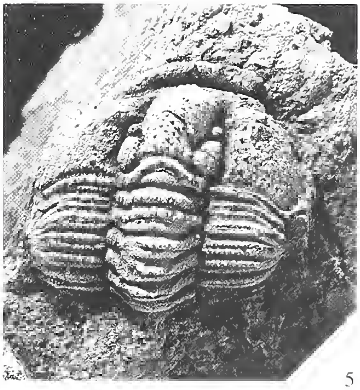

3


4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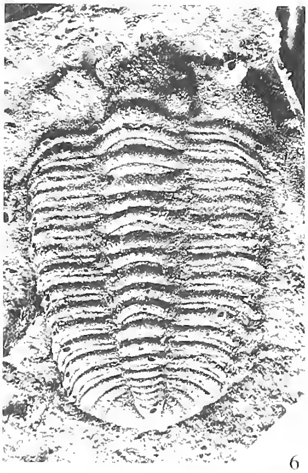
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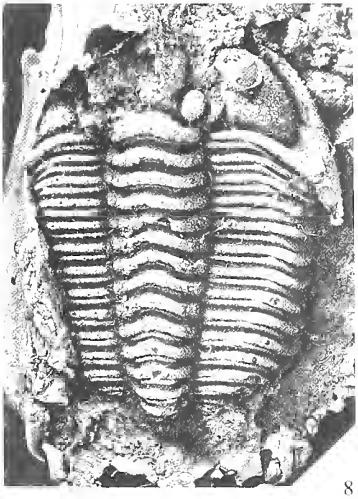
7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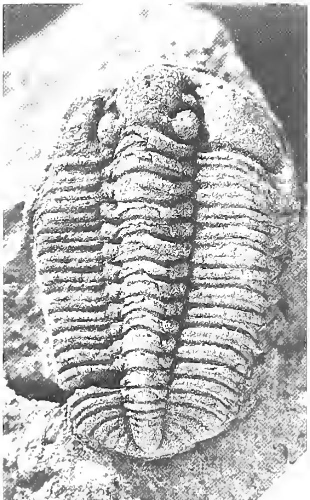
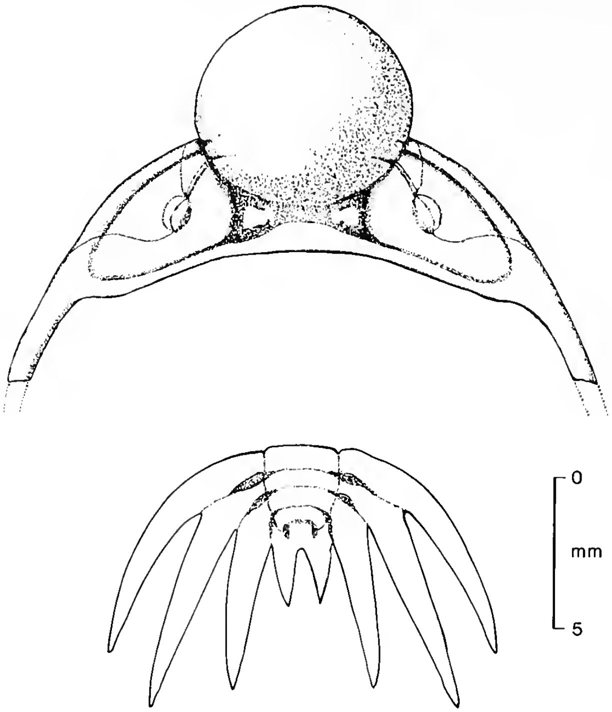

9

ROMANO, *Prionocheilus*



TEXT-FIG. 5. *Actinopeltis tejoensis* sp. nov. Reconstruction of cephalon and pygidium.

spaced tubercles. Prominent eye on short stalk, situated on highest part of cheek and fairly close to posterior border furrow. Eye lenses visible on QXP. 2.002. Well marked, low, eye ridge runs from eye to axial furrow just anterior to where S2 starts. Anterior branch of facial suture runs anterolaterally from the eye, approximately parallel to axial furrow, to margin. Posterior branch curves outwards and then backwards in even curve to cut lateral margin just anterior to base of genal spine. Lateral and posterior border furrows deep, except around base of genal spine. Posterior border convex (exsag.); narrowest near midline, widening evenly and gradually to genal spine. Free and fixed cheek covered with coarse pits of irregular size and distribution.

Thorax consists of eleven segments. Axis narrow, strongly convex, and delimited by rather weak axial furrows. Axial rings gently curved forwards, broadest (sag.) along mid-line. Rings consist of convex (sag. and trans.) posterior band which broadens laterally. Anterior part of ring consists of broad, nearly flat band which narrows toward axial furrow where there is a shallow apodeme. Convex articulating half-ring separated from axial ring by marked change of slope. Pleurae consist of inner part (approximately one-third their transverse width) which is flat lying, and an outer spinose part which is outwardly inclined. Inner part of pleural segment consists of wide (exsag.), convex band bounded by narrow anterior and posterior bands. Wide band carries rows of pits, generally about 6, along midlength (appears as almost continuous groove on internal mould). Posterior pleural band is constricted at the fulcrum, where there is a prominent fulcral process and socket. Axial rings carry fairly dense ornament of faint tubercles while spinose parts of pleurae are very sparsely tuberculate.

Pygidial axis about one and a half times as long as wide, delimited by shallow furrows which become less well defined posteriorly. Axis consists of 4 rings which decrease in length posteriorly. Ring furrows shallow medially. Posterior to fourth axial ring are pair of short, longitudinally aligned furrows which lie in series with the deeper inner parts of pleural furrows. Pleurae consist of inner flattish part in which, from front to back, pleurae are progressively directed more posteriorly. Pleural furrows end in deep apodemal pits at axis. Outer parts of pleurae are slender spines; the first two being long, slightly curved and approximately of equal length; the third is a little shorter and curved proximally, while the fourth pair are much shorter (about one-quarter as long as second pair and less than half as long as third pair), more slender and directed backwards. In one specimen (QXP. 2.029*a*, *b*) the fourth pair of spines are considerably longer than in the other two examples and extend posteriorly to terminate level with the tips of the third pair. Axis and flat pleural region carry a few scattered tubercles while the spines have an ornament similar to that of the glabella.

Discussion. The genus had previously been recorded in Portugal from Valongo and Buçaco. At Valongo, Curtis (1961) recorded *A. wattisoni* sp. nov. (referred to *Valongia wattisoni* by Přibyl and Vaněk 1984) which differs from the Mação species in possessing 12 thoracic segments, a less swollen median glabellar lobe, more forwardly placed eyes and shorter genal spines. The 'faint horizontal rib furrow' which Curtis (1961, p. 9) described appears to consist of a row of faint pits as in the present material (see Curtis 1961, plate 4). Also, the pygidial rib furrows on *wattisoni* may be deformational features. At Buçaco, Delgado (1908, p. 57) listed a number of '*Cheirurus*' species from the upper Ordovician, some of which have been more recently described by Thadeu (1947). Of these, *A*. aff. *completa* (Barrande) (Thadeu 1947, pl. 3, figs 6 and 7) from the Porto de Santa Anna Formation has been recently compared to *A. vercingetorix* Přibyl and Vaněk (1969) by Hammann (1974, p. 105). Both of these species show a more forwardly placed eye and coarser sculpture on the glabella than *Actinopeltis tejoensis*. *A. spjeldnaesi* (Hammann 1972, p. 372, pl. 1, fig. 3; 1974, p. 102, pl. 12, figs 200–207, text-fig. 38; 1976, p. 65, pl. 5, figs 64–68) from the upper Caradoc–lower Ashgill (Hammann *et al*., 1982, p. 23) of Almadén (Sierra Morena, Spain) is fairly close to *A. tejoensis*. Rábano (1984) considered *A. spjeldnaesi* to be of Caradoc age. The Spanish species possesses more forwardly placed eyes, basal glabellar lobes which are not clearly delimited adaxially, and lacks the broad (sag.) furrow posterior to the swollen part of the glabella. The anterior pygidial spines are also more outwardly flexed in *A. spjeldnaesi*. It is of interest to note, however, that in both *A. spjeldnaesi* and *A. tejoensis* the fourth pair of pygidial spines are of variable length (see Hammann 1974, pl. 12, fig. 203; 1976, fig. 65; and Pl. 3, figs 7, 11 herein). This characteristic appears to be independent of preservation.

Delgado (1908) first recorded the Mação species as '*Cheirurus* sp. n. aff. *gryphus* Barrande' (Barrande 1872, pl. 3, figs 10–17) but the Bohemian specimens clearly differ from the Portuguese material in having less prominent eyes situated closer to the glabella and considerably shorter genal spines. Among other Bohemian species of *Actinopeltis*, the type species, *A. globosa* (Barrande 1852, pl. 35, figs 1–7, pl. 40, figs 26 and 27, pl. 43, fig. 27; Whittington 1968, text-fig. 7, p. 104), and the closely related *A. rivanol* (Šnajdr, 1982) have less well delimited L1 adaxially, and shorter genal and pygidial spines; the latter being well rounded distally. *A. insocialis* (Barrande, 1852, pl. 40, figs 28–31) does not possess genal spines, and the pygidial spines are shorter and rounded at the ends. Kielan (1959) assigned the specimens of *A. insocialis* from the Králův Dvur beds to a new species, *A. barrandei*, which also differs from *Actinopeltis tejoensis* in the absence of genal spines, the very small eye and the only slightly pointed pygidial spines. *Actinopeltis* sp. 'a' from the *S. clavifrons* Zone of Poland (Kielan 1959, pl. 24, fig. 4, text-fig. 36) has a similar structure to the pygidial axis as *Actinopeltis tejoensis* but the tuberculation is coarser and more densely spaced.

Genus VALONGIA Přibyl and Vaněk, 1984

Type species. *Actinopeltis wattisoni* Curtis, 1961.

Valongia wattisoni (Curtis, 1961)

*1961	*Actinopeltis wattisoni* sp. nov.; Curtis, p. 8, pl. 3, fig. 2, pl. 4, fig. 1.
1974	*Actinopeltis wattisoni* Curtis; Hammann, p. 105.
1982	*Actinopeltis wattisoni*; Romano, p. 96.
1984	*Valongia wattisoni* (Curtis); Přibyl and Vaněk, p. 126, fig. 4, 3.

Material. In 49184, holotype, part and counterpart of nearly complete specimen.

Horizon and locality. Upper part of Valongo Formation, near Covelo; Llandeilo.

Discussion. The species was described and figured by Curtis (1961) and no further material has been found. Curtis assigned the species to *Actinopeltis*. Recently Přibyl and Vaněk (1984) erected a new genus, *Valongia*, for this species since they considered the specimen showed important morphological features which distinguished it from those assigned to *Actinopeltis*. These included size of free cheek, course of facial suture, position of palpebral lobes, number of axial segments and structure of pygidial axis. The present author is in agreement with Přibyl and Vaněk that Curtis' species shows significant differences from those of *Actinopeltis*, but is more reluctant to follow their procedure of erecting a new genus, based on a single deformed specimen. However, for the present, their proposal is followed here.

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After this manuscript was completed the author was kindly sent an important paper by Rábano (1990) on middle Ordovician trilobites of the Central Iberian Zone in Spain. Rábano recognized *S. lusitanica* (Thadeu, 1949) as a distinct species and pointed out that it was distinguishable from *S. salteri* by a number of cephalic features (Rábano 1990, pp. 120–122). However, the variability of the sculpture and the frequently deformed nature of the Portuguese specimens do not allow confident separation of these two forms. Rábano also stated that *S. lusitanica* is a characteristic species of the Lower Llanvirn of the Central Iberian Zone, and designated the specimen figured by Thadeu (1949), pl. 2, fig. 1) as the lectotype. This specimen (SG ?1688) was collected from '1650 m [not 1680 m] S 20° O da piramide de Santa Justa (Valongo)'. From the same locality, *Eccoptochile almadenensis*, *E.* cf. *clavigera* and *Eodolmanitina ?destombesi destombesi* occur. The known ranges of these three species indicate a Llandeilo age for this assemblage.

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CAMBROCLAVES AND PARACARINACHITIDS, EARLY SKELETAL PROBLEMATICA FROM THE LOWER CAMBRIAN OF SOUTH CHINA

by S. CONWAY MORRIS *and* CHEN MENGE

ABSTRACT. Cambroclaves are a major group of sclerite-bearing metazoans, known from the Lower Cambrian of China (south China, Xinjiang), USSR (Kazakhstan) and Australia. *Zhijinites longistriatus* Qian is redescribed on the basis of abundant material from the Hongchunping Formation at Maidiping, Sichuan. Sclerites show extensive morphological variability and have a taphonomic history of endolithic infestation and diagenetic phosphatization, the latter leading to replication of wall ultrastructure. *Deiradoclavus trigonus* gen. et sp. nov. and *Deltaclavus graneus* gen. et sp. nov. are younger cambroclaves recovered from the Guojiaba Formation near Kuanchuanpu, Shaanxi, and the Shuijingtuo Formation at Taishanmiao, Hubei. Both taxa bore a cataphract scleritome, composed of interlocking sclerites. In *Deltaclavus* articulated series of sclerites include 'arm-like' structures. Paracarinachitids may be related to cambroclaves, and are described on the basis of isolated sclerites of *Paracarinachites spinus* Yu from the Yuhucun Formation of Meishucun, Yunnan. *Protopterygotheca leshanensis* Chen from the Hongchunping Formation of Maidiping is included in the paracarinachitids, and is described on the basis of isolated sclerites bearing prominent flanges on either side of the spatulate axis. The primary function of the scleritomes of cambroclaves and paracarinachitids may have been protective, but in the absence of intact scleritomes both the palaeoecology and affinities of these groups are uncertain. The new class Cambroclavida is proposed.

THE irruption of skeletal faunas close to the Precambrian–Cambrian boundary (Conway Morris 1987, 1989*a*) has attracted wide attention on two principal counts. First, there is debate as to whether the acquisition of skeletons (*a*) was mediated by extrinsic factors, such as changes in ocean chemistry, and/or (*b*) represents a biological response such as providing a defensive cover against durophagous predators and offering greater support to soft tissues. The second point of discussion is the part these early skeletal faunas played in the major adaptive radiations that are often referred to as the 'Cambrian explosion'. Evidence for metazoan diversification is readily apparent from both the record of trace fossils (Crimes 1989) and Burgess Shale-type soft-bodied assemblages (Conway Morris 1989*b*), but by taphonomic necessity the bulk of the evidence must come from skeletal remains. It has become apparent that many of the earliest of these forms are of problematic affinity, bearing no clear relationship to known phyla. Although some taxa continue to languish in a taxonomic limbo, recent work has demonstrated the presence of several major groups. All are extinct, but their status probably deserves the cognomen, in terms of orthodox taxonomy, of phylum on account of their distinctive body-plans (but see Conway Morris 1989*c*). Such groups now include the tommotiids, coeloscleritophorans, anabaritids, cambroclaves and the possibly related paracarinachitids, the last two of which are the subject of this paper. With the exception of the tubicolous anabaritids, all these groups share a skeletal arrangement of sclerites that presumably coated the exterior body to form the scleritome. Reconstruction of the original scleritome ideally relies on articulated material such as might occur in a Konservat-Lagerstätte. With the halkieriids (Coeloscleritophora) comparisons with the Burgess Shale *Wiwaxia* allowed the latter to act as a model for scleritome reconstruction (Bengtson and Conway Morris 1984), and this may now be tested further on account of the discovery of articulated halkieriids in the Lower Cambrian of north Greenland (Conway Morris and Peel 1990). In the remaining cases, however, sclerite arrangement must be inferred from either rare specimens showing fusion or functional analysis of areas of articulation between adjacent sclerites.

[Palaeontology, Vol. 34, Part 2, 1991, pp. 357–397, 9 pls.]

CAMBROCLAVES

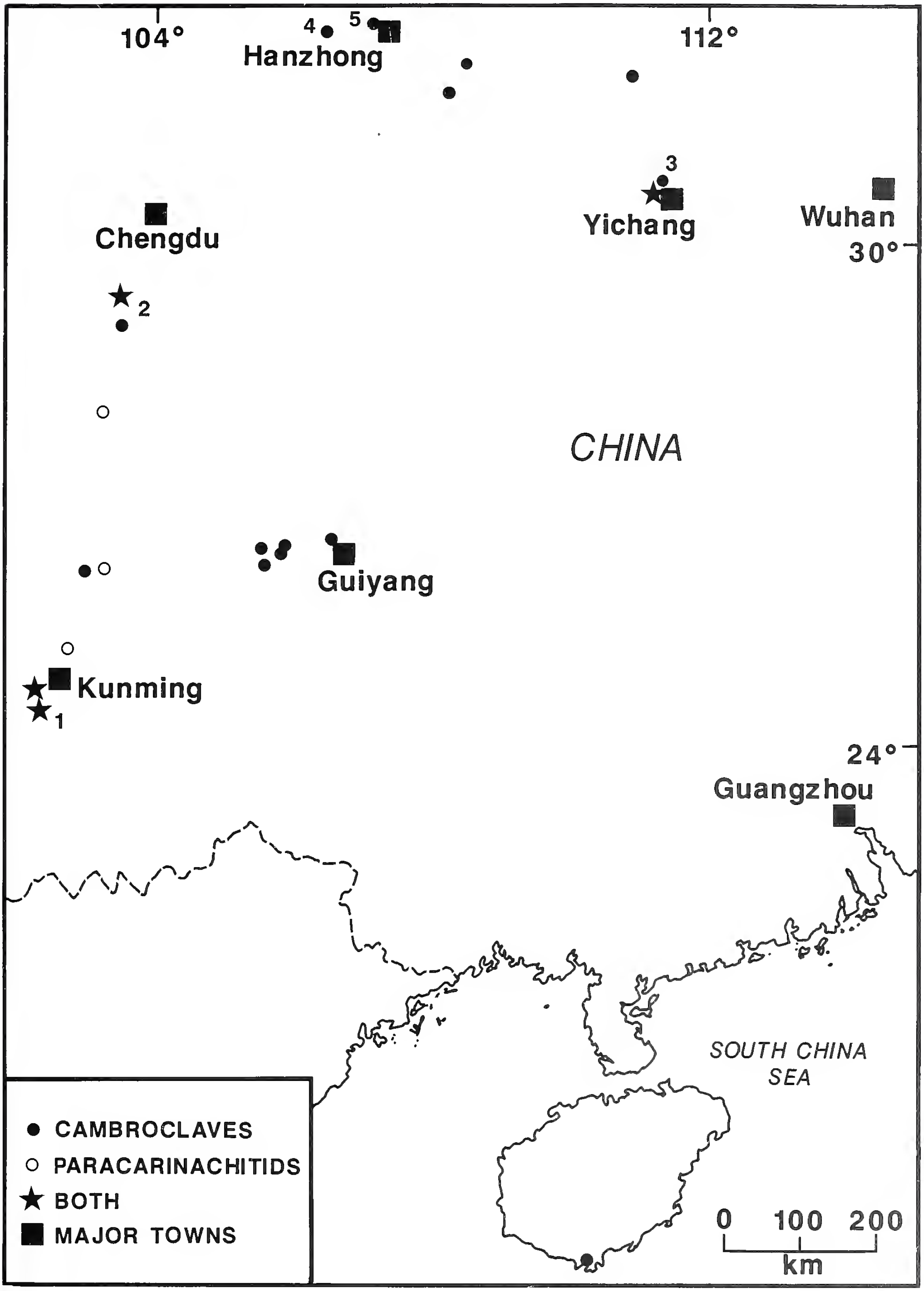
Cambroclaves are represented by a distinctive group of sclerites that consist of a circular to oval base that bears a spine, usually elongate. They are recorded from the Lower Cambrian of China (Text-fig. 1), Kazakhstan, and Australia. However, they appear to be unknown from other parts of the world, including the equivalent-aged sections in Mongolia, the Siberian platform, and Canada. In the past, it has been found useful to make a distinction between sclerites with a sub-circular base bearing a prominent spine (zhijinitid morph) and those with a more elongate base, often having a dumb-bell shape, with the spine arising from the anterior half (cambroclavid morph). The orientation of cambroclaves follows that outlined by Mambetov and Repina (1979, fig. 8), with the prominent spine assumed to arise from the anterior end of the dorsal surface. In the absence of any articulated scleritomes, overall sclerite attitude with respect to the entire animal, assumed to be a bilaterally symmetrical metazoan, is not known.

Scleritomes that appear to have consisted of either entirely zhijinitids or predominantly cambroclavids with a small proportion of zhijinitids are both known. The former type is documented in some detail here on the basis of Chinese material of *Zhijinites longistriatus* Qian, while cambroclavids have received extensive study on the basis of well-preserved material of a new species of *Cambroclavus* from South Australia (Bengtson *et al.* 1990). Reconstructions of cambroclave scleritomes may also be inferred with varying degrees of confidence from descriptions in the literature. However, the wide morphological variability of the sclerites has resulted in excessive use of form-taxa by some authors, and one aim of the extensive synonymy list proposed here for *Z. longistriatus* is to encourage a classification designed to lead to more reliable scleritome reconstructions. In addition to the two basic sclerite types mentioned above, two other variants are reported on the basis of scleritomes inferred to have consisted of (*a*) oval sclerites bearing a ridge-like spine (*Deiradoclavus* gen. nov.), and (*b*) sclerites with a predominantly triangular outline (*Deltaclavus* gen. nov.).

The first report of cambroclaves was by Zhong [Chen] (1977), who mentioned and illustrated material from Guizhou and Sichuan provinces as *Zhijinites* sp. However, as none of the formalities of his taxonomic description accords to those laid down by the International Commission for Zoological Nomenclature, this reference to *Zhijinites* must be taken as a nomen nudum. Formal descriptions of *Zhijinites* (*Z. longistriatus*, *Z. minutus*), on the basis of material from near the town of Zhijin, west of Guiyang in Guizhou Province (Text-fig. 1), were made available shortly afterwards by Qian (1978*a*, see also 1978*b*). This and adjacent localities in Guizhou have continued to provide abundant material of *Zhijinites* (Chen 1979; Qian and Yin 1984*a*, *b*; Wang *et al.* 1984*a*, *b*), as have other localities (Text-fig. 1) in Sichuan (Chen 1979; Yin *et al.* 1980*a*, *b*; Yang *et al.* 1983; He *et al.* 1984), Yunnan (Jiang 1980, 1982; Luo *et al.* 1984*a*) and Hubei provinces (Chen 1979; Qian *et al.* 1979). Numerous species of *Zhijinites* have been erected, most of which are probably synonymous (see below). In addition the genera *Heterosculpotheca* Jiang, 1982 and *Parazhijinites* Qian and Yin 1984*b*, are both regarded as junior synonyms of *Zhijinites*. Furthermore, what are evidently specimens of *Zhijinites* have been referred to the conodont-like *Fomitchella* (Yin *et al.* 1980*a*), the halkieriid *Sachites* (Yin *et al.* 1980*a*) and the hyolith *Allatheca* (Yang *et al.* 1983).

Notwithstanding the taxonomic confusion that appears to accompany our existing understanding of *Zhijinites* from south China, in the majority of samples it seems that the sclerites are derived from the dispersal of a scleritome composed exclusively of zhijinitid morphs. There is, however, evidence

TEXT-FIG. 1. Distribution of cambroclaves and paracarinachitids in China. The numbers refer to localities from which material described herein has been recovered: 1, Meishucun, Yunnan (see Text-fig. 6); 2, Maidiping, Sichuan (see Text-fig. 3); 3, Taishanmiao, Hubei (see Text-fig. 5); 4, Xuanjiangping, Shaanxi; 5, Liangshan, Shaanxi (for both see Text-fig. 4). In addition to these occurrences cambroclaves are reported also from Xinjiang province, China (Qian and Xiao 1984), Kazakhstan, USSR (Mambetov and Repina 1979) and Australia (Bengtson *et al.* 1990). Paracarinachitids are reported also by Kerber (1988) from southern France.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that in some stratigraphically higher cambroclaves such morphs persisted as a minor component in a scleritome otherwise composed of cambroclavid sclerites. For example, in reconstructing an Australian cambroclave the occasional zhijinitid morphs were regarded as an integral part of the scleritome (Bengtson *et al.* 1990). This decision was based on the presence of intermediate forms which showed a progressive reduction of the posterior end, general similarities of ornamentation, and consistent co-occurrence with the more abundant cambroclavid morphs. It is for this reason that a number of Chinese species placed in *Zhijinites* are regarded tentatively as more probably being derived from a cambroclavid scleritome, rather than once constituting a scleritome composed of only zhijinitids. One such instance might be *Z. intermedius*, and perhaps *Z. claviformis*, from the Lower Cambrian Yurtus Formation of Xinjiang Province (Qian and Xiao 1984) that could be attributable to the same scleritome that yielded elements referred to *Cambroclavus* (= *Sugaites*) *bicornis*. Similarly, zhijinitid morphs (*Z. claviformis*, *Z. cordiformis*) co-occurring with cambroclavid sclerites in the upper Lower Cambrian (Damao Group) of Yaxian County, Hainan Island (Text-fig. 1) (Jiang and Huang 1986) may all be derived from the same scleritome. Duan (1984) described zhijinitid-morphs, which he attributed to *Tanbaoites* (*T. porosus*, *T. spiculosus*) from the Xihaoping Formation of Hubei Province (Text-fig. 1). However, they co-occur with a plethora of cambroclavid taxa (nine species placed in *Cambroclavus*, *Sinoclavus* and *Phyllochiton*) that may all be derived from a single scleritome. What may be similar cambroclavids have also been recorded from strata of Atdabanian age from a section at Xiaoyangba in Zhenba County, Shaanxi (Text-fig. 1) (Xie 1988, fig. 1).

It is clear, therefore, that until a more rigorous approach to scleritome reconstruction in Chinese cambroclaves is undertaken, little headway can be expected in draining the swamp of form-taxonomy that mires present efforts to introduce a degree of order. This is also exemplified in the interpretation of cambroclaves from Maly Karatau and Talassky Ala-Too, Kazakhstan (Mambetov *in* Mambetov and Repina 1979; see also Missarzhevsky and Mambetov 1981). Mambetov provided the first description of the cambroclave morph in the form of *Cambroclavus antis*. In addition a zhijinitid-morph was distinguished as *C. undulatus*, which both Jiang (1982) and Duan (1984) transferred to *Zhijinites*. As the stratigraphic range of *C. antis* and *Z. undulatus* only partly overlap, it is possible that each was derived from a separate scleritome. It is also conceivable, however, that the concept of *Z. undulatus* is incompletely understood. Zhijinitid-morphs that co-occur with *C. antis* (Mambetov *in* Mambetov and Repina 1979, pl. 13, figs 2, 10, 13) appear to differ from those collected from a separate horizon (Mambetov *in* Mambetov and Repina 1979, pl. 13, figs 1, 4, 11, 12), and it may be that only the latter belong to *Zhijinites* s.s., having been derived from a scleritome composed solely of zhijinitids. Yet another type of cambroclave, *Pseudoclavus singularis* (Mambetov *in* Mambetov and Repina 1979, pl. 14, figs 5, 7, 10, 11) represents a distinctive variety of cambroclave, apparently unique to Kazakhstan. The status of the remaining taxon, *C. clavus*, described by Mambetov *in* Mambetov and Repina (1979, pl. 13, figs 3, 5, 7–9), is somewhat uncertain, but it seems to be a zhijinitid-like morph with a conspicuous spine and diminished base.

Although sclerites are almost invariably found isolated owing to both post-mortem decay of any intervening soft tissue and the exigencies of the extraction technique of acid digestion and sieving, their original arrangement may be preserved in rare instances as fused associations. These were noted first by Mambetov (*in* Mambetov and Repina 1979, pl. 14, figs 6, 8, 9) who depicted sclerites of *C. antis* deployed in orderly rows. Amongst the well-preserved cambroclavids from the Atdabanian Ajax Limestone of South Australia rare examples of two sclerites fused in a longitudinal direction were noted (Bengtson *et al.* 1990). Such specimens confirm the function of the anterior ventral and posterior dorsal facets. In addition, outline shape of these Australian cambroclavids shows how they would have interlocked to form a cataphract (chainmail-like) arrangement (Text-fig. 11 B), and this lends credence to the idea that the sclerites might have formed a protective coating on a metazoan. Analogies to the wiwaxiids and halkieriids, where entire specimens are known, might suggest that cambroclaves were also worm or slug-like. However, unusual examples of articulated series of sclerites in *Deltaclavus graneus* gen. et sp. nov. (see below) and lack of knowledge of associated soft parts makes these analogies distinctly tentative.

The analysis of the new Australian species of *Cambroclavus* also revealed the sclerites to have a very wide degree of morphological variability, encompassing not only radical differences in typical cambroclavid types, but also reduction towards a zhijinitid condition of sub-circular base surmounted by prominent spine (Bengtson *et al.* 1990). While the possibility cannot be dismissed that any one individual bore a restricted range of sclerite morphs, it is considered more likely that mutual accommodation in shape between adjacent sclerites would have led to extensive variation across the body. For the most part, published illustrations of cambroclaves are insufficient to gauge reliably the extent of morphological variability. However, the likelihood of extensive synonymies within suites of sclerites, ostensibly belonging to a plethora of nominal taxa, from localities such as Hubei (Duan 1984; Qian and Yin 1984*b*) and Xinjiang provinces (Qian and Xiao 1984) argue for morphological variability being widespread in cambroclaves.

PARACARINACHITIDS

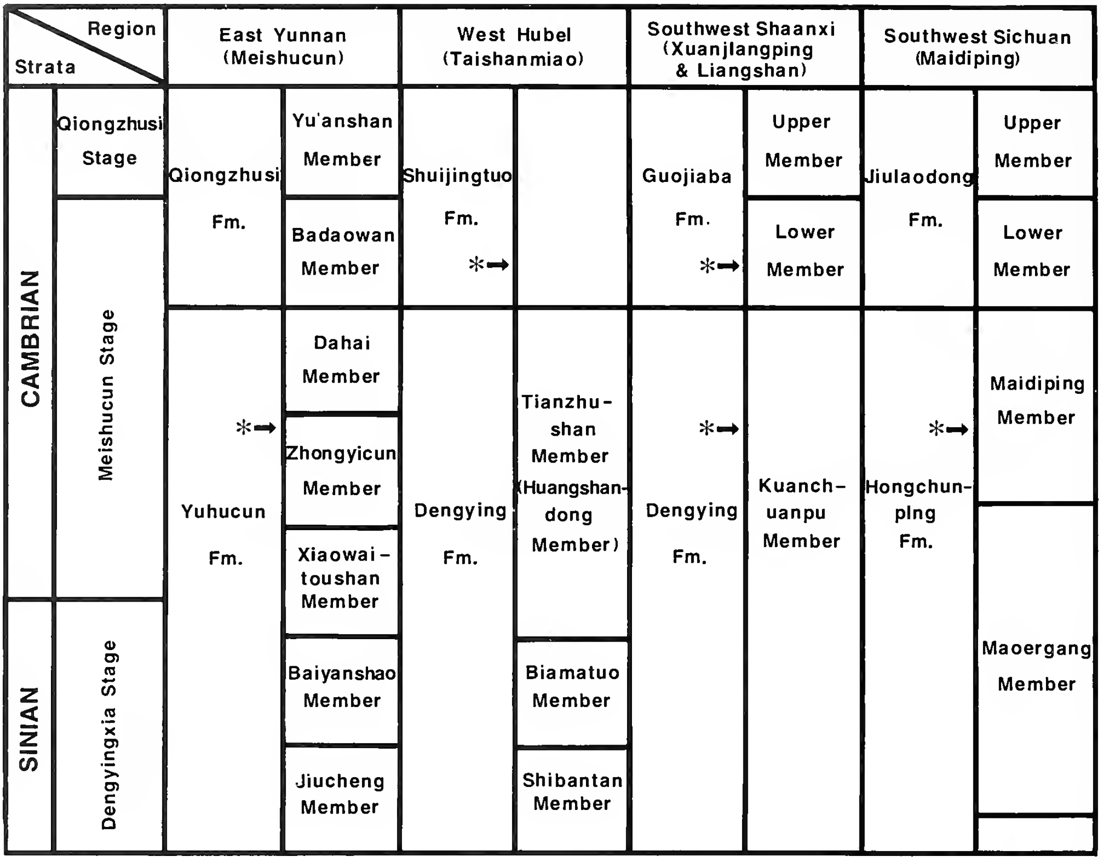
These distinctive sclerites have been reviewed critically by Qian and Bengtson (1989), who recognized four species (the type species *Paracarinachites sinensis*, and also *P. columellatus*, *P. parabolicus* and *P. spinus*). Paracarinachitids have a narrow spatula-like form with a median row of spines, and evidently grew incrementally. Although best known from South China (Qian and Bengtson 1989), sclerites from the Montagne Noire of southern France are important because they show also a flange (Kerber 1988). Here, we describe material probably attributable to *P. spinus*, but differing in occurring as single sclerites rather than articulated associations where the sclerites are arranged in a row. In *Protopterygotheca leshanensis* Chen in Qian *et al.*, 1979 sclerite form is especially clear on account of well-developed flanges, but the diagnostic paracarinachitid spines are only seldom evident. Ultimately it may transpire that *Protopterygotheca* Chen, 1979, should be taken as a senior synonym of *Paracarinachites* Qian and Jiang, 1982 (see Qian and Bengtson 1989), but this is premature on existing evidence. Qian and Bengtson (1989) proposed that paracarinachitids and zhijinitids are closely related. This may well be correct for *P. spinus*, but the remaining three species of *Paracarinachites* (and the related sclerites of *Protopterygotheca* and *Scoponodus*) may be better treated as a group distinct from the cambroclaves. In addition, the possibility that *Ernogia* (see Qian and Bengtson 1989, pp. 100–102, figs 64 and 65) be included in the roster of paracarinachitids may also bear further consideration. Qian and Bengtson (1989) considered this option briefly, on account of both overall shape and growth incrementation. The nodular ornamentation on the exterior of *Ernogia* stands in contrast to the median spines of *Paracarinachites*, but this difference may be of relatively minor importance given the more or less smooth appearance of most sclerites of *P. leshanensis* described herein.

STRATIGRAPHY AND LOCALITIES

The material described herein comes from the following horizons and localities:

1. *Zhijinites longistriatus*. All the material illustrated here was obtained from Beds 36 and 37 of the Maidiping Member, Hongchunping Formation (Text-fig. 2), exposed at the Maidiping section near to Emei, Sichuan Province (Text-fig. 3). This section is one of many Precambrian–Cambrian Boundary sections located around Emei Mountain (see He *et al.* 1984, fig. 4-1), but its stratigraphy and fossil content have received particularly detailed attention by several workers (e.g. Yin *et al.* 1980*a*, *b*; He and Yang 1982; He *et al.* 1984). Zhijinitids were reported by Zhong [Chen] (1977, p. 123), Chen (1979, p. 281), and Yin *et al.* (1980*a*, pp. 178–179; see also synonymy list for apparently erroneous assignments to *Fomitchella* and *Sachites hastatus*).

Comparable material was obtained from the Dananguo section, Liangshan (Text-fig. 4), located 3 km from the Oriental Instrument Plant factory and 10 km north-west of Hanzhong (Fu 1983, fig. 1; Ding *et al.* 1983, fig. 2). Here the Yangjiakon member of the Dengying Formation (Text-fig. 2) (Fu's placement of this part of the section in the Guojiaba Formation is less likely, because correlations suggest it to be equivalent to the deeper water Kuanchuanpu Member exposed west of Hanzhong in the Ningqian area (see Xing and Yue 1984; Conway Morris and Chen 1989)) is composed near its top of sandy glauconitic limestones. It yields abundant zhijinitids (Fu 1983; Ding *et al.* 1983) which, however, are generally somewhat smaller than those recovered



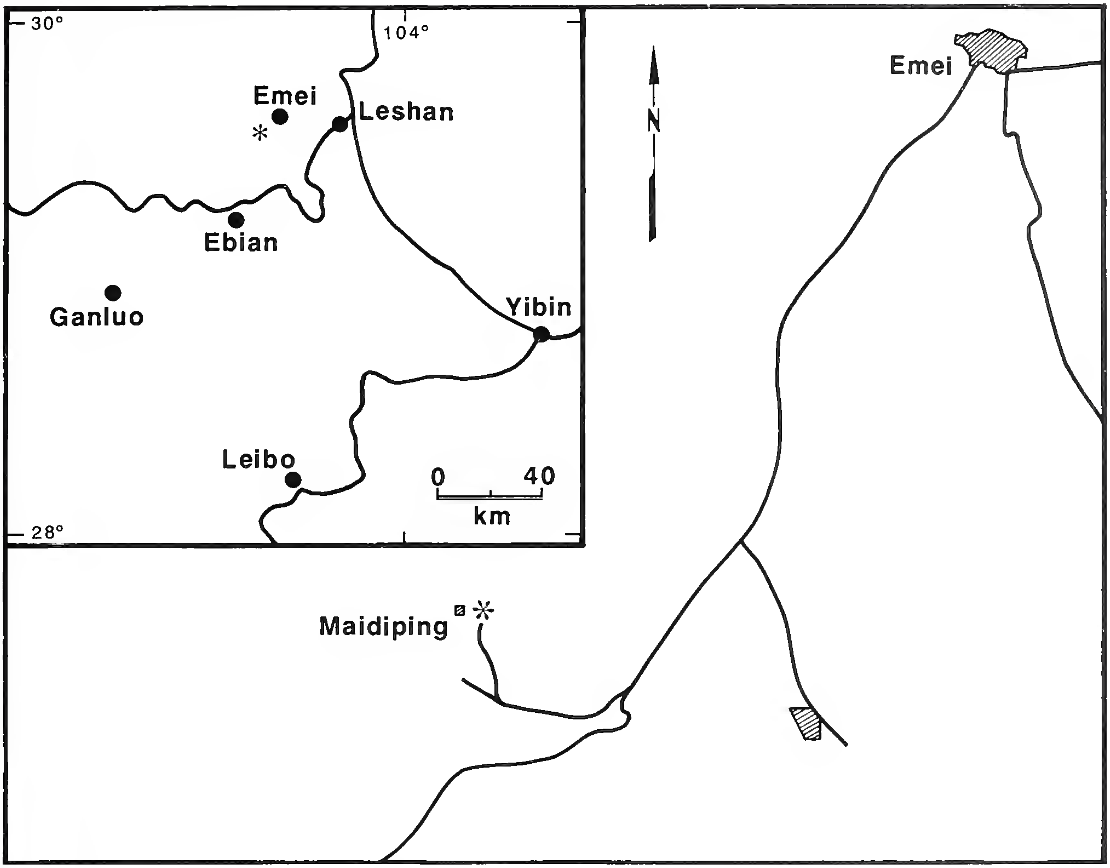
Strata \ Region		East Yunnan (Meishucun)		West Hubel (Taishanmiao)		Southwest Shaanxi (Xuanjlangping & Liangshan)		Southwest Sichuan (Maidiping)	
CAMBRIAN	Qiongzhusi Stage	Qiongzhusi Fm.	Yu'anshan Member	Shuijingtuo Fm. *→		Guojiaba Fm. *→	Upper Member	Jiulaodong Fm.	Upper Member
	Meishucun Stage		Badaowan Member				Lower Member		Lower Member
		Yuhucun Fm. *→	Dahai Member	Dengying Fm.	Tianzhushan Member (Huangshandong Member)	Dengying Fm. *→	Kuanchuanpu Member	Hongchunplng Fm. *→	Maidiping Member
			Zhongyicun Member						
			Xiaowaitoushan Member						Maoergang Member
SINIAN	Dengyingxia Stage		Baiyanshao Member		Biamatuo Member				
			Jiucheng Member		Shibantan Member				

TEXT-FIG. 2. Summary stratigraphic chart for the Sinian–Cambrian boundary sequence in South China (see Text-fig. 1 for position of localities). Asterisked arrows refer to stratigraphic horizons of occurrence of cambroclaves and paracarinachitids, see text for further details. Based on table 8-1 of Ding *et al.* (1984).

from Maidiping. In addition to zhijinitids the productive sample yielded also abundant *Hyolithellus*, rare *Protohertzina* (cf. Fu 1983) and spicules. From the overlying shales of the Guojiaba Formation (equivalent to the Qiongzhusi Formation) at Liangshan Chen (1985) has described trilobites.

2. *Deiradoclavus trigonus* gen. et sp. nov. Abundant specimens were recovered from a calcareous horizon (thin limestones overlying beds with calcareous concretions) in the otherwise largely clastic Guojiaba Formation (Text-fig. 2) (see Chen *et al.* 1975, fig. 2). The outcrop forms part of the Xuanjiangping section, and is located in a stream about 1500 m southeast of the hamlet of Xuanjiangping (Text-fig. 4). The underlying strata, especially of the Kuanchuanpu Formation, have received extensive attention on account of their abundant small skeletal fossils and proximity to the Precambrian–Cambrian Boundary (e.g. Shizhonggou section, Xing and Yue 1984; Xing *et al.* 1984; Piaojiaya section (Text-fig. 4), Conway Morris and Chen 1989). However, apart from reports of *Tommotia* (Qin and Yuan 1984), the small skeletal fossils of the Guojiaba Formation appear to have received little attention. In addition to *Deiradoclavus* the sample yielded *Tannuolina zhangwentangi* (Conway Morris and Chen 1990*b*; Qin and Yuan's (1984) report on *Tommotia* may refer to this taxon), *Pelagiella* sp., *Actinotheca*, bradoriids, unidentified tubes, and other problematica.

3. *Deltaclavus graneus* gen. et sp. nov. Abundant material was recovered from the lower Shuijingtuo Formation (Text-fig. 2; see also Zhou and Xu 1987), exposed in the Taishanmiao section, near the village of Taishanmiao, Hubei Province (Text-fig. 5). The sample was a fallen block in a roadside quarry about 250 m south of the Precambrian–Cambrian Boundary as locally defined within the Tianzhushan member of the

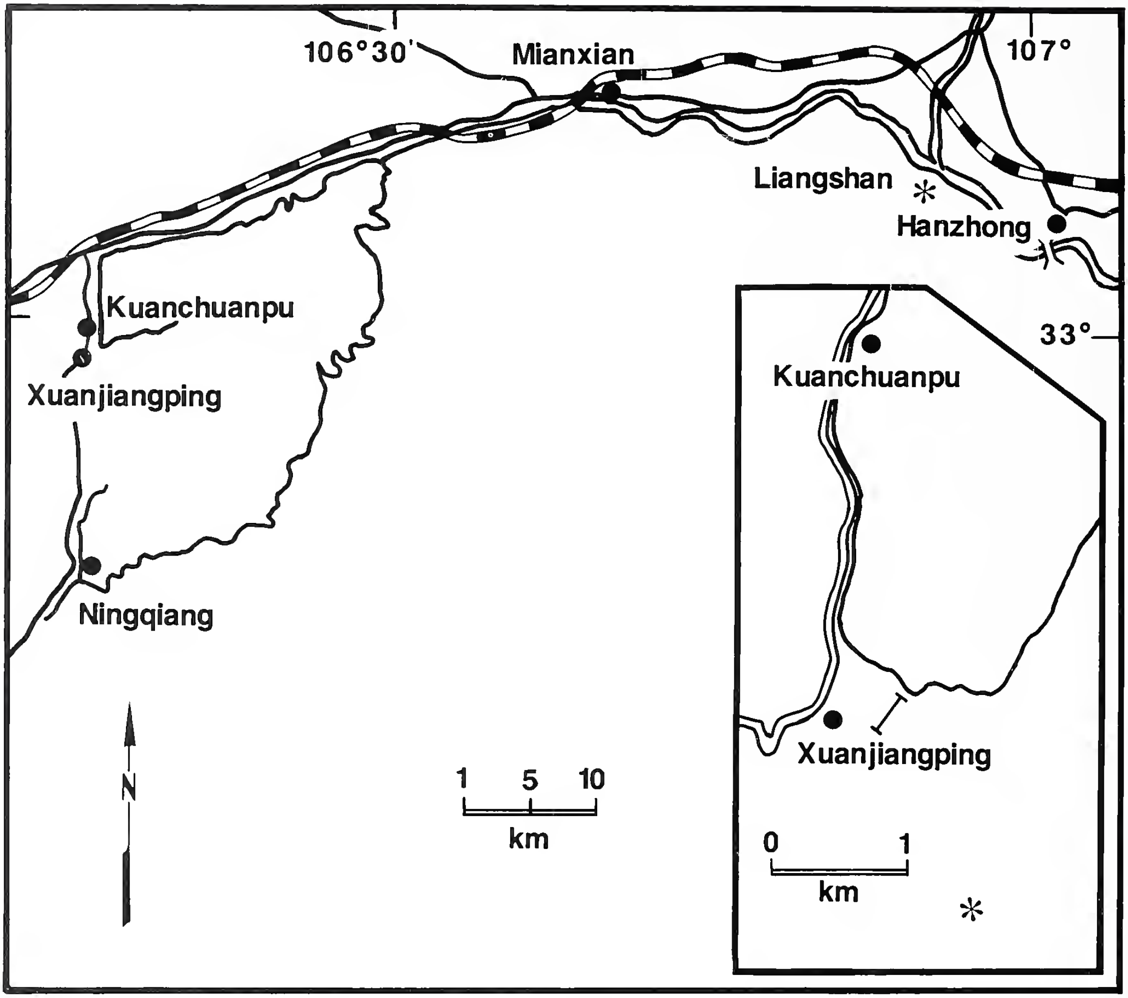


TEXT-FIG. 3. Locality map of region around Emei (Sichuan), showing location of Maidiping section (asterisked). Based on fig. 1 of Yin *et al.* (1980*b*) and fig. 4.1 of He *et al.* (1984).

Dengying Formation (see Conway Morris and Chen (1990*a*) for further details of locality and associated fauna, including the problematic *Blastulospongia*).

Despite a variety of stratigraphic terms, for the most part correlation of the Lower Cambrian around the Yangtze platform of South China (Text-fig. 2) is reasonably straightforward (e.g. Xing *et al.* 1984). Accepting the existing scheme of correlations it would appear that the zhijinitids from Maidiping (Sichuan) and Meishucun (and Liangshan, Shaanxi) are of approximately the same age, falling into the lower part of the *Paragloborilus–Siphogonuchites* assemblage. *Deiradoclavus* gen. nov. from the lower Guojiaba Formation (Shaanxi) and *Deltaclavus* gen. nov. from the lower Shuijingtuo Formation are somewhat younger, and about the same age as one another. These two genera appear to be closely related, and it is to be expected that similar cambroclaves will be found in due course in equivalent strata such as the Badaowan member of the Qiongzhusi Formation (Yunnan) and the Jiulaodong Formation (Sichuan) (Text-fig. 2). These are predominantly clastic units, but so far investigation of carbonate horizons in both formations (Conway Morris and Chen, 1990*b*; see also Qian and Bengtson 1989) has not revealed any material.

4. *Paracarinachites spinus*. Numerous specimens were recovered from dolomites of Bed 7 of the Zhongyicun member, Yuhucun Formation (Text-fig. 2) exposed at the Xiawaitoushan section of the Kunyang Phosphorite Mine, at Meishucun, Yunnan Province (Text-fig. 6) (Luo *et al.* 1980, 1982, 1984*a*, *b*). The Meishucun locality has attracted widespread interest on account of it being the Chinese stratotype candidate for the Precambrian–Cambrian Boundary. To date, this taxon has been chiefly documented from articulated series of sclerites from this horizon and the overlying Bed 8 of the Dahai Member (Text-fig. 2) (see Qian and Bengtson



TEXT-FIG. 4. Locality map of region near Hanzhong (Shaanxi), showing locations of section near Liangshan (asterisk on main map) and near Xuanjiangping (asterisk on inset map), and also Piaojiaya section (see Conway Morris and Chen 1989). Based on fig. 6-1 of Xing and Yue (1984).

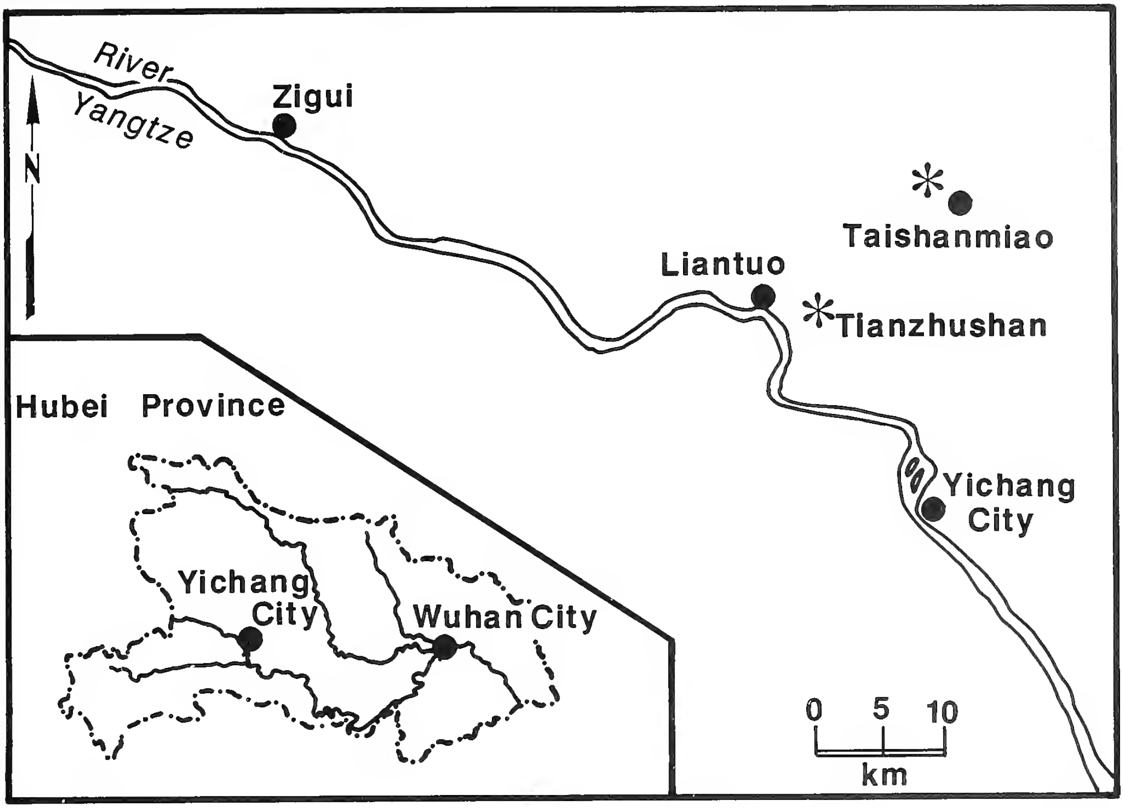
1989; He and Xie 1989), and the abundant isolated sclerites are less well known (He and Xie 1989, pl. 1, figs 20 and 22).

5. *Protopterygotheca leshanensis*. This material, which only seldom has the median spines diagnostic of other paracarinachitids present, was obtained from the same horizons at Maidiping, Emei (Text-fig. 3) as the specimens of *Z. longistriatus* (see above). The type material of this taxon comes from the Tianzhushan section in Hubei (Text-fig. 5).

SYSTEMATIC DESCRIPTIONS

Class CAMBROCLAVIDA nov.

Diagnosis. Calcareous(?) sclerites with variously shaped base bearing an elongate spine, forming a scleritome that ranged from articulated cataphract array to individual sclerites studding surface, apparently separated by unmineralized tissue.



TEXT-FIG. 5. Locality map of region around Yichang (Hubei), showing location of Taishanmiao and Tianzhushan sections (asterisked). Based on fig. 2-1 of Chen *et al.* (1984).

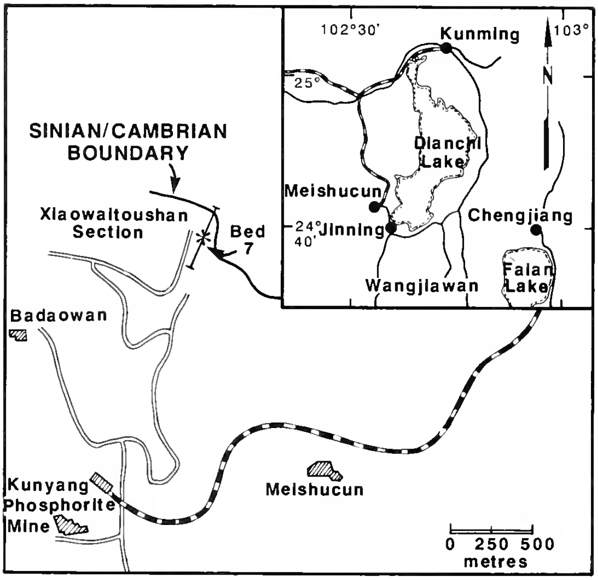
Family ZHIJINITIDAE Qian, 1978*a*

Emended diagnosis. Sclerites composed of base and elongate spine, now hollow, formerly filled with soft tissue? Base may be subcircular to elongate. In the latter case it may have prominent constriction imparting dumb-bell shape, and usually articulatory facets. Dorsal surface ornamentation frequently of radiating low ridges. Spine elongate, usually recurved posteriorly, transverse section varies from circular to elongate. Original composition probably calcareous.

Component genera. (1) *Zhijinites* Qian, 1978*a* (junior synonyms include *Sachites* sensu Yin *et al.*, 1980*a*, *non* Meshkova, 1969; *Fomitchella* sensu Yin *et al.*, 1980*a*, *non* Missarzhevsky *in* Rozanov *et al.*, 1969; *Heterosculpotheca* Jiang, 1982; *Parazhijinites* Qian and Yin, 1984*b*). (2) *Cambroclavus* Mambetov *in* Mambetov and Repina, 1979 (junior synonyms include *Phyllochiton* Duan, 1984; *Sinoclavus* Duan, 1984; *Sugaites* Qian and Xiao, 1984; and probably *Isoclavus* Qian and Zhang, 1983; *Tanbaoites* Duan, 1984; *Wushichites* Qian and Xiao, 1984; and *Zhijinites* (in part) sensu Qian and Xiao, 1984; and Jiang and Huang, 1986; see above). (3) *Deiradoclavus* gen. nov. (4) *Deltaclavus* gen. nov.

ZHIJINITES Qian, 1978*a*

Type species. Zhijinites longistriatus Qian, 1978*a*.



TEXT-FIG. 6. Locality map of region around Meishucun (Yunnan), showing location of Bed 7 of the Xiaowaitoushan section (asterisked). Based on figs 1 and 2 of Luo *et al.* (1984*b*).

Diagnosis. Sclerite base subcircular to somewhat elongate, ventral base gently concave, dorsal surface convex. Margin usually entire, occasionally with prominent cleft that may be enclosed to leave perforation. Spine elongate, inclined, more or less straight. Transverse section of spine variable from subcircular to concavo-convex, ornamentation variable, including prominent transverse ridges, longitudinal ribbing to more or less smooth.

Zhijinites longistriatus Qian, 1978*a*

Plates 1–3; Text-figs 7 and 11*a*

1977 *Zhijinites* sp. Zhong [nomen nudum], p. 123, pl. 3, fig. 7; pl. 4, figs 22–27.
1978*a* *Zhijinites longistriatus* Qian, p. 34, pl. 2, fig. 5*a*, *b*.
1978*b* *Zhijinites longistriatus* Qian, p. 350, pl. 142, fig. 5*a*, *b*.
1978*a* *Zhijinites minutus* Qian, p. 34, pl. 2, fig. 6*a*–*c*.
1978*b* *Zhijinites minutus* Qian, p. 350, pl. 142, fig. 4*a*–*c*.
1979 *Zhijinites annae* Chen [nomen nudum], p. 281, fig. 3*d*.
1979 *Zhijinites costatus* Chen [nomem nudum], p. 281, fig. 3*b*.
1979 *Zhijinites dictyoformise* Chen [nomen nudum], p. 281, fig. 3*e*.
?1979 *Zhijinites lubricus* Qian *et al.*, p. 225, pl. 4, figs 14 and 15.
1979 *Zhijinites minutus* Lu, pl. 1, figs 6 and 7.
1979 *Zhijinites longistriatus* Lu, pl. 1, figs 19 and 20; pl. 2, figs 2 and 11.
?1980 *Zhijinites lubricus* Zhao *et al.*, p. 49, pl. 3, fig. 21.
?1980*a* *Zhijinites lubricus* Yin *et al.*, p. 178, pl. 19, figs 11 and 12.
1980*a* *Zhijinites longistriatus* Yin *et al.*, p. 179, pl. 19, figs 8 and 10.
1980*a* *Zhijinites minutus* Yin *et al.*, p. 179, pl. 19, fig. 9.
?1980*a* *Fomitchella* sp. Yin *et al.*, pl. 19, fig. 7.
1980*a* *Sachites hastatus* Yin *et al.*, p. 195, pl. 18, fig. 9 (?non pl. 18, fig. 30).
?1980*b* *Zhijinites lubricus* Yin *et al.*, p. 65.
1981 *Zhijinites minutus* Xiang *et al.*, pl. 1, fig. 15.
1982 *Zhijinites longistriatus* Yin *et al.*, pp. 287, 291.

1982 *Zhijinites minutus* Yin *et al.*, pp. 287, 291.
1982 *Zhijinites longistriatus* Jiang, p. 181, pl. 17, figs 8, 9, 19.
?1982 *Zhijinites lubricus* Jiang, p. 182, pl. 17, fig. 13.
1982 *Zhijinites minutus* Jiang, p. 182, pl. 17, figs 6, 7, 20.
?1982 *Zhijinites undulatus* Jiang, p. 182, pl. 17, fig. 11 (non fig. 12, 12*a* ? = *Paracarinachites spinus*).
?1982 *Zhijinites umbelletes* Jiang, p. 182, pl. 17, fig. 10, 10*a*.
1982 *Heterosculpotheca pheneres* Jiang, p. 166, pl. 13, figs 23, 23*a*, 24, 25.
?1983 *Zhijinites lubricus* Fu, p. 416, pl. 1, figs 12 and 13.
?1984 *Zhijinites lubricus* Qian, pl. 3, fig. 8.
1984 *Zhijinites minutus* Qian, pl. 3, fig. 7.
?1984 *Zhijinites* sp. Qian, pl. 3, fig. 16.
?1983 *Allatheca nanjiangensis* [nomen nudum] Yang *et al.*, p. 95, pl. 1, fig. 14.
1984*a* *Zhijinites longistriatus* Qian and Yin, pl. 4, fig. 14.
1984*a* *Zhijinites minutus* Qian and Yin, pl. 5, fig. 14.
1984*b* *Zhijinites longistriatus* Qian and Yin, pp. 215, 218, pl. 1, figs 12–15.
1984*b* *Zhijinites cordiformis* Qian and Yin, pp. 215, 219, pl. 1, figs 20–23.
1984*b* *Zhijinites minutus* Qian and Yin, pp. 215, 218, text-figs 1.3 and 3*c*.1, 2; pl. 1, figs 1–11.
1984*b* *Zhijinites panduriformis* Qian and Yin, pp. 215, 218, 219, pl. 1, figs 16–19.
1984*b* *Zhijinites triangularis* Qian and Yin, pp. 215, 219, pl. 2, figs 14–21.
?1984*b* *Parazhijinites quizhouensis* [sic] Qian and Yin, p. 220, text-fig. 3.3; pl. 2, figs 1–8.
1984*a* *Zhijinites longistriatus* Wang *et al.*, pl. 22, figs 13 and 14.
1984*a* *Zhijinites minutus* Wang *et al.*, pl. 22, figs 1–4.
1984*a* *Zhijinites panduriformis* Wang *et al.*. p. 177, pl. 22, figs 9–12.
?1984*a* *Parazhijinites guizhouensis* Wang *et al.*, p. 177, pl. 22, figs 5-8.
1984*b* *Zhijinites longistriatus* Wang *et al.*, pl. 4, fig. 9.
1984*b* *Zhijinites minutus* Wang *et al.*, pl. 5, fig. 14.
1984*a* *Zhijinites minutus* Luo *et al.*, pl. 10, fig. 24.
1984 *Heterosulpotheca* [sic] *phaneres* [sic] Jiang, fig. 4.3.
1984 *Heterosulpotheca* [sic] *phoneres* [sic] Jiang, pl. 2, fig. 8.
1984 *Zhijinites minutus* Jiang, pl. 3, fig. 11.
?1987 *Parazhijinites quizhouensis* [sic] Liu, fig. 3A.
?1987 *Zhijinites triangularis* Liu,, fig. 3B.
1989 *Zhijinites* sp. Chen, pl. 1, fig. 1.

Diagnosis. As for the genus.

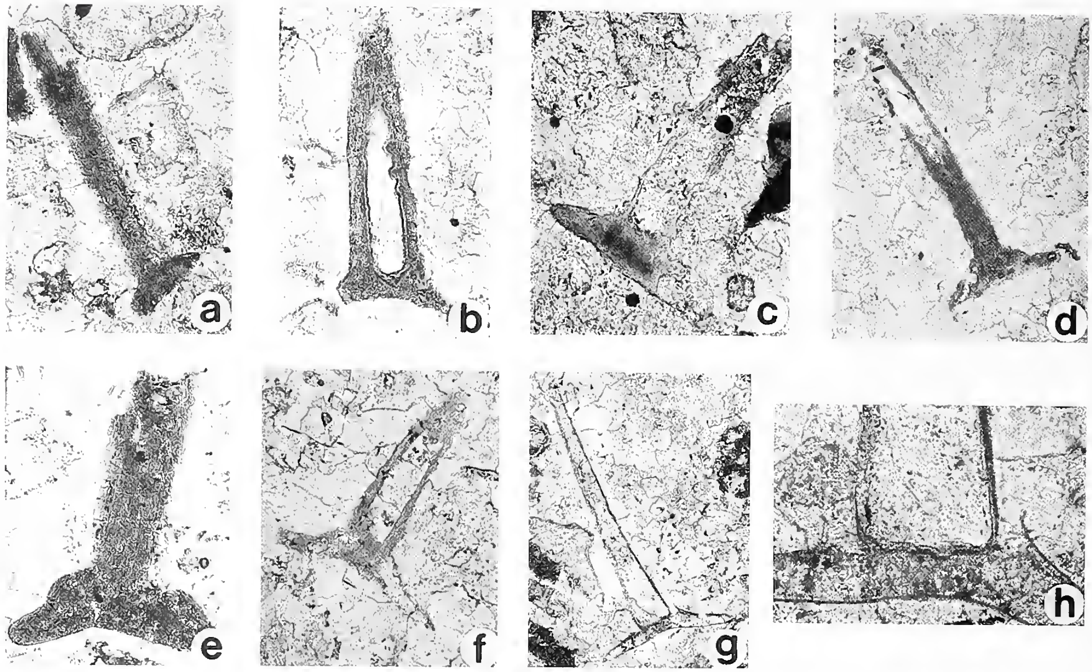
Holotype. Institute of Geology and Palaeontology, Academia Sinica, Nanjing, ASN 33676 (Qian 1978*a*, pl. 2, fig. 5).

Material illustrated here. Institute of Geology (Beijing), Academia Sinica IGAS-BC-88-30079-30112.

Stratigraphic horizon. Beds 36 and 37, Maidiping Member, Hongchunping Formation, Meishucun Stage, Lower Cambrian (see Yin *et al.* 1980*a*, *b* and He *et al.* 1984 for further details).

Locality. Maidiping section, Emei, Sichuan.

Preservation. The majority of specimens consist of sclerites with a phosphatized wall enclosing a central cavity (Text-fig. 7). Petrographic sections demonstrate that the extent of phosphatization varies quite widely, and may include obvious spherulitic ingrowths on the interior of the spine cavity (Text-fig. 7*b*). The dorsal side of the base is, apart from radial furrows, often relatively smooth (e.g. Pl. 1, figs 1, 3, 16, 17; Pl. 2, figs 4, 8, 13). It is frequent on the spine, however, for surfaces to be more irregular, consisting of a fibrous ultrastructure running parallel to the long axis of the spine (Pl. 1, figs 5, 11–14, 16; Pl. 2, figs 1 and 10). This fibrosity is interpreted as diagenetic phosphatization of an originally calcareous wall. In addition, endolithic borings are also abundant in some specimens. These may be visible as openings on the surface of the base (Pl. 1, figs 8 and 9), or as steinkerns of tubes that run along the spine (Pl. 3, figs 1–3, 9, 12). The tubes consist of two distinct size classes (*c.* 3 μm and 7 μm diameter respectively). The larger category possesses a series of swellings, sometimes locally pronounced, that impart a beaded appearance (Pl. 3, figs 10 and 13) and may end blindly



TEXT-FIG. 7. Petrographic thin sections of *Zhijinites longistriatus* Qian, 1978 from Beds 36 (*a–c*, *e*, *g* and *h*) and 37 (*d*, *f*), Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China, to show varying degrees of diagenetic phosphatization. *a*, IGAS-BC-88-30199, distal portion of spine abraded, × 66. *b*, IGAS-BC-88-30200, note spherulitic growths into central cavity, × 66. *c*, IGAS-BC-88-30201, note abraded tip and incomplete phosphatization, × 45. *d*, IGAS-BC-88-30202, × 38. *e*, IGAS-BC-88-30203, × 22. *f*, IGAS-BC-88-30204, note incomplete phosphatization of base, × 43. *g* and *h*, IGAS-BC-88-30205; *g*, note restricted degree of phosphatization, × 33; *h*, detail of proximal area with septum between cavities of spine and base respectively, × 135.

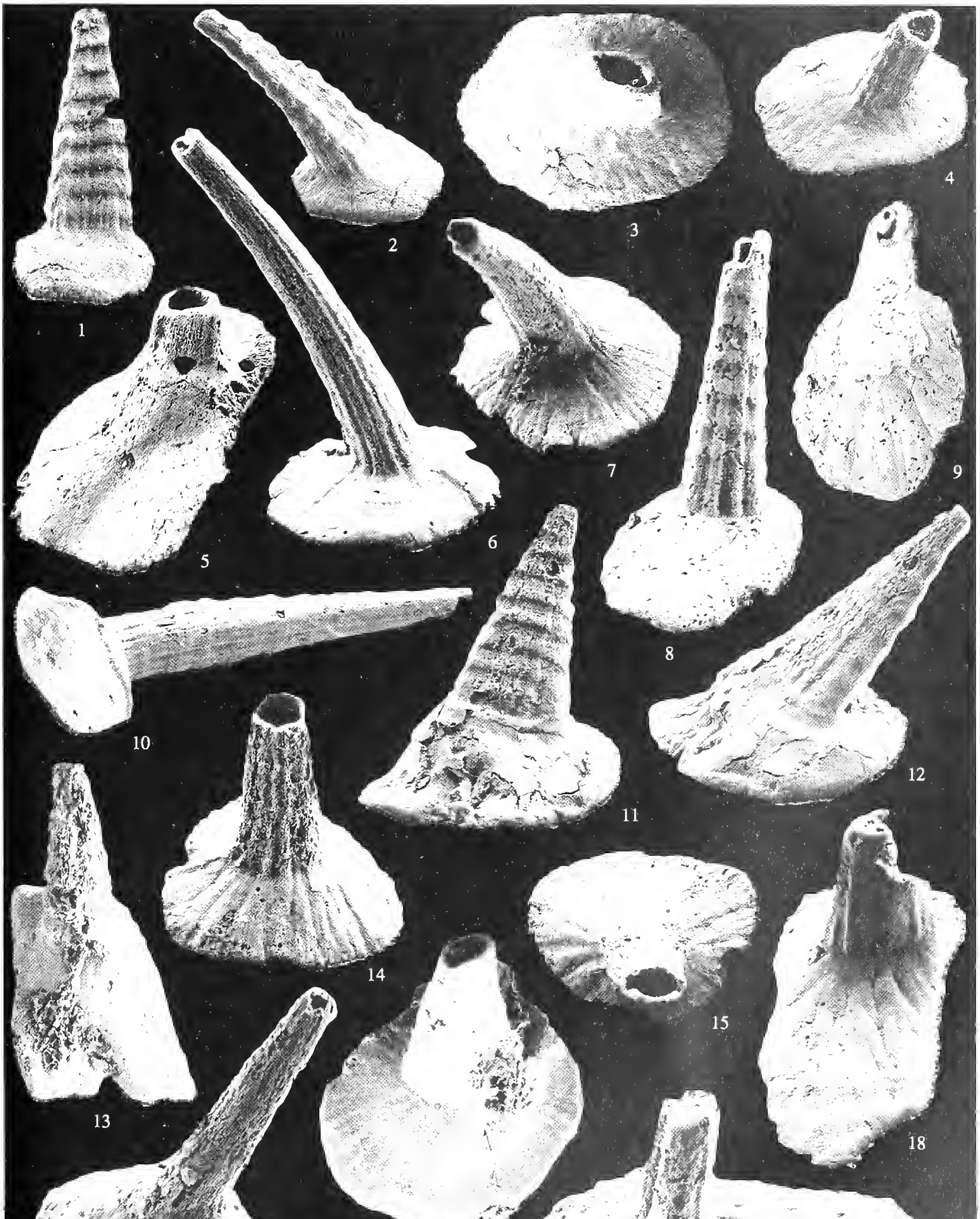
(Pl. 3, fig. 7). The borings run sub-parallel, but may recurve or arch over each other near points of contact (Pl. 3, fig. 11). The smaller tubes are generally more filiform (Pl. 3, figs 10 and 11), may show branching and only locally possess swellings in diameter.

The other principal type of preservation is as steinkerns of the spine (Pl. 2, fig. 16; Pl. 3, figs 4–6). These were regarded as a separate taxon, referred to as *Heterosculpotheca pheneres* by Jiang (1982, pl. 13, figs 23, 23*a*, 24, 25), which is taken here as a junior synonym of *Zhijinites longistriatus*. Their origin can be confirmed, both from Jiang's (1982) illustrations (especially his pl. 13, figs 23*a* and 25) which show the characteristic transverse ornamentation of the spines, and the identical ultrastructure of the steinkern surface as seen in isolated specimens and in exposed patches beneath the wall of more complete individuals (see Runnegar 1985 for similar examples of ultrastructural replication). The ultrastructure consists of longitudinal lineations that have a stepped appearance along irregular re-entrants (Pl. 2, fig. 17; Pl. 3, figs 8, 10, 13). In addition the surface bears elongate pores (Pl. 3, fig. 4) that mark the course of tubes that enter the steinkern at shallow angles.

EXPLANATION OF PLATE 1

Figs 1–19. *Zhijinites longistriatus* Qian, 1978. 1 and 2, IGAS-BC-88-30079. 3 and 4, IGAS-BC-88-30080. 5, IGAS-BC-88-30081. 6 and 7, IGAS-BC-88-30082. 8 and 9, IGAS-BC-88-30083. 10, IGAS-BC-88-30084. 11 and 12, IGAS-BC-88-30085. 13, IGAS-BC-88-30086. 14 and 15, IGAS-BC-88-30087. 16, IGAS-BC-88-30088. 17, IGAS-BC-88-30089. 18 and 19, IGAS-BC-88-30090. All isolated sclerites from Bed 36, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnification all × 70.

PLATE 1



CONWAY MORRIS and CHEN, *Zhijinites*

Description. The overall form of a circular base bearing an elongate spine is subject to considerable degrees of morphological variation (Pl. 1, figs 1–19; Pl. 2, figs 1–9, 11–15). The basal unit is concave–convex, and in the majority of specimens more or less circular. However, elongate and more irregular forms (Pl. 1, figs 5, 18, 19; Pl. 2, figs 7 and 15) are also known. A more persistent trait is the presence of an embayment or notch on the anterior/posterior margin (Pl. 1, figs 13 and 16). In most specimens there is only a single embayment, but occasionally several occur adjacent to one another in one sclerite. In some individuals this feature is open, but in others it is tightly incised so that ultimately it consists of a perforation through the base, connected to the margin by a ligatural line (Pl. 2, fig. 6).

The concave ventral side of the base appears to have been smooth (Pl. 1, fig. 10; Pl. 2, fig. 5), but the dorsal surface characteristically bears an ornamentation of irregular furrows (Pl. 1, figs 3, 4, 6–9, 14–19; Pl. 2, figs 4, 10, 11). Where the base is circular these furrows have a radial disposition, whereas in more elongate sclerites the ornamentation shows a corresponding linearity.

The elongate spine generally arises eccentrically, although whether nearer to the anterior or posterior margin depends on possible homologies with the cambroclavid sclerites. If the spine is anterior, as in cambroclavids (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990), then in contrast to the cambroclavids the zhijinitid spine was sometimes inclined anteriorly (e.g. Pl. 1, figs 4, 9, 16; Pl. 2, figs 3, 8, 12, 13). If the spine is posterior, then the marginal notch (when present) would be consistently located on the anterior margin (Pl. 1, figs 13 and 16; Pl. 2, fig. 6), whereas in cambroclavids it is usually on the posterior margin (e.g. Qian and Zhang 1983, pl. 3, figs 9, 11, 12, 14, 16; Duan 1984, pl. 5, figs 16*a*, *b* and 17*a*, *c*; Qian and Xiao 1984, pl. 1, figs 7 and 13; pl. 3, figs 11, 16, 18; see Bengtson *et al.* 1990 for proposed synonymies of the taxa erected by these Chinese workers).

In the majority of sclerites the area of insertion of the spine occupies a relatively small proportion of the dorsal surface (Pl. 1, figs 3, 4, 6, 15; Pl. 2, figs 4 and 11). In a few individuals the ratio between spine and base is greatly increased (Pl. 2, figs 1 and 9), although incomplete margins often make it difficult to determine the exact proportions. The spine arises from the base at varying angles, ranging from more or less right angles (Pl. 1, fig. 19; Pl. 2, figs 9 and 15) to about 45°, the latter being more common. The distal end of the spine is almost invariably absent, but it is clear that the length varied and bears no simple relationship to diameter of the base. In a longitudinal direction the spine is usually more or less straight, but recurved instances are also known (Pl. 2, fig. 14). In transverse section the spine varies between circular (e.g. Pl. 1, figs 6 and 16) to distinctly elongate (at right angles to the antero-posterior axis), sometimes with a more or less prominent groove on one margin. Most typically the ornamentation of the spine consists of prominent transverse welts that impart a ribbed appearance (Pl. 1, figs 1, 2, 8, 11). In some sclerites a subsidiary longitudinal ornamentation gives a more nodular appearance to the spine (Pl. 2, figs 3, 7, 8, 12), while in some spines the surface bears only longitudinal lineations (Pl. 1, figs 6, 10, 14). In this last case, care must be exercised between recognizing an original ornamentation and a spine where loss of the outer layers (Pl. 1, figs 5 and 16) has affected the original pattern and imparted a subdued longitudinal fibrosity that stems from exposure of the wall ultrastructure (see above).

Discussion. The wide morphological variation of the sclerites has been interpreted by previous workers as representing several discrete taxa, which have been distinguished principally upon the criteria of spine ornamentation and spine length. The co-occurrence of morphs ascribed to a number of nominal species in our samples and the continuity of variation suggest that many, if not all, these sclerites were derived from a single species, here recognized on grounds of priority as *Z. longistriatus*. Specimens with spines bearing longitudinal ribbing have been attributed by previous workers mostly to either *Z. longistriatus* or *Z. costatus*, while those with transverse folds have been

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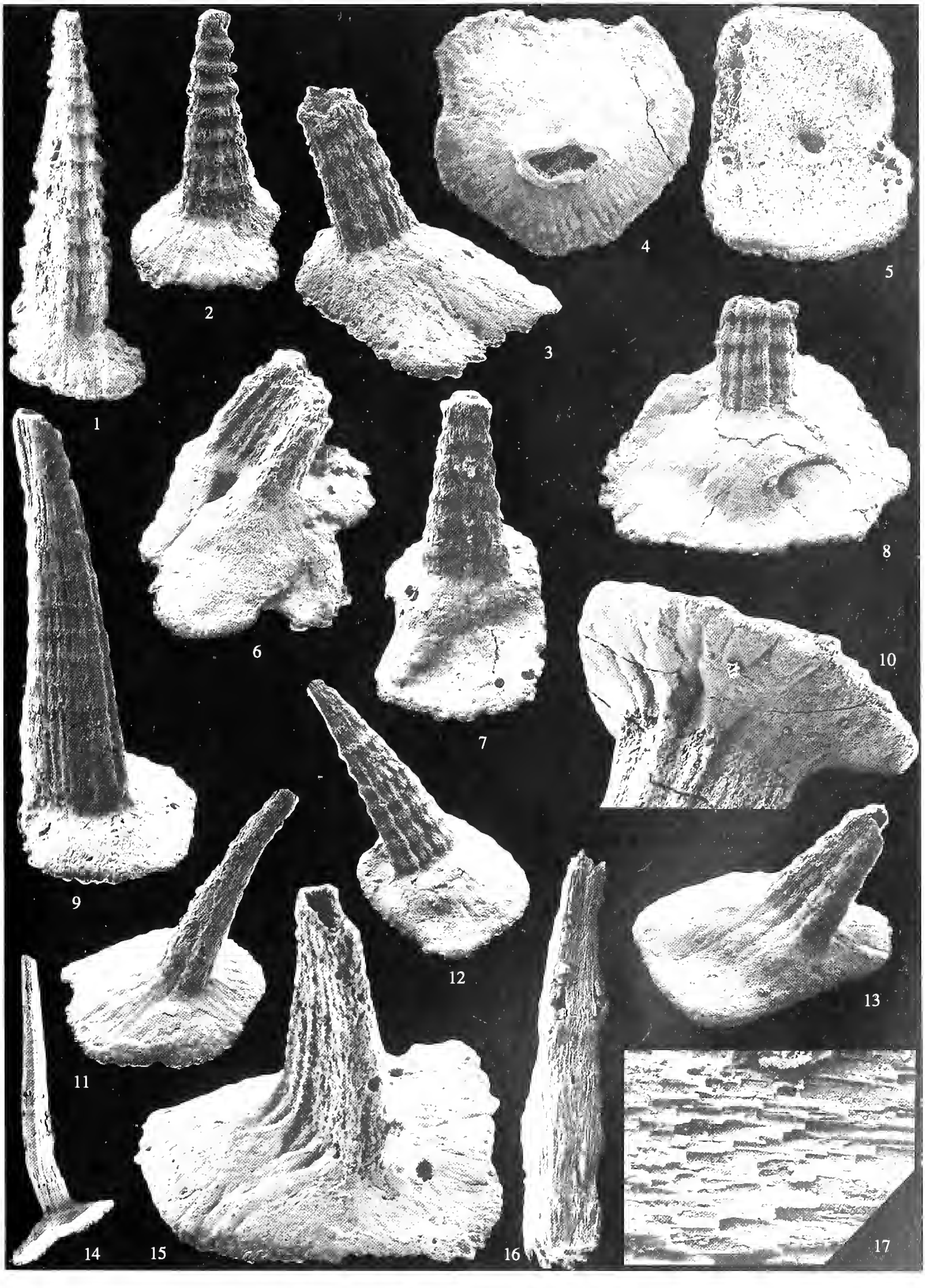
EXPLANATION OF PLATE 2

Figs 1–17. *Zhijinites longistriatus* Qian, 1978. 1, IGAS-BC-88-30091. 2, IGAS-BC-88-30092. 3, IGAS-BC-88-30093. 4, IGAS-BC-88-30094. 5, IGAS-BC-88-30095, ventral surface. 6, IGAS-BC-88-30096. 7, IGAS-BC-88-30097. 8, IGAS-BC-88-30098. 9, IGAS-BC-88-30099. 10, IGAS-BC-88-30100. 11, IGAS-BC-88-30101. 12, IGAS-BC-88-30102. 13, IGAS-BC-88-30103. 14, IGAS-BC-88-30104. 15, IGAS-BC-88-30105. 16 and 17, IGAS-BC-88-30106; 16, steinkern of spine cavity; 17, detail of steinkern surface showing possible replication of wall ultrastructure. All isolated sclerites from Bed 37, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications all × 70, except Fig. 10 (× 100), Fig. 14 (× 35), and Fig. 17 (× 700).

PLATE 2



CONWAY MORRIS and CHEN, *Zhijinites*

placed in at least four nominal species (*Z. annae* [nomen nudum], *Z. dictyformise* [nomen nudum], *Z. minutus* and *Z. triangularis*). The synonymy of certain other species with *Z. longistriatus* remains less certain. Sclerites with more or less smooth spines have been placed mostly in *Z. lubricus*, while sclerites with a slipper-like base and very elongate spine have been named as *Parazhijinites guizhouensis* (sometimes misspelt *quizhouensis*).

If the extensive synonymies proposed above are accepted, albeit some being provisional, then it remains to be decided whether an individual possessed a corresponding range of sclerite types or whether the variability was greater between animals, with any one individual showing a more restricted degree of variation. In the absence of either articulated individuals or fused sclerites (see below), these alternatives remain unresolved. However, as a working hypothesis it is proposed that morphological variability of sclerites in any one individual was pronounced.

If it was possible to provide an adaptive explanation for the different sclerite types, especially with respect to spine angle and spine ornamentation, then one might hypothesize further about the possible distribution of the sclerites over the body. In discussing cambroclaves from the Lower Cambrian of Australia, Bengtson *et al.* (1990) suggested the sclerites were used to grip the sediment, as well as providing a protective function. If *Zhijinites* had a similar mode of life, then it seems possible that the inclined spines served to provide anchors on the sediment during locomotion. It is suggested further that the transverse corrugations (Pl. 1, figs 1, 2, 11; Pl. 2, figs 1–3, 7–9, 12) acted as a ratchet-like device to increase frictional contact with the sediment grains. In this context those spines with a more subdued ornamentation may have occupied regions of the body that were not directly involved with acting as anchors. Concerning the varying angles the spines make with the basal unit, and by implication the surface of the body, this could be linked to local configurations of the epithelium.

DEIRADOCLAVUS gen. nov.

Type species. Deiradoclavus trigonus gen. et sp. nov.

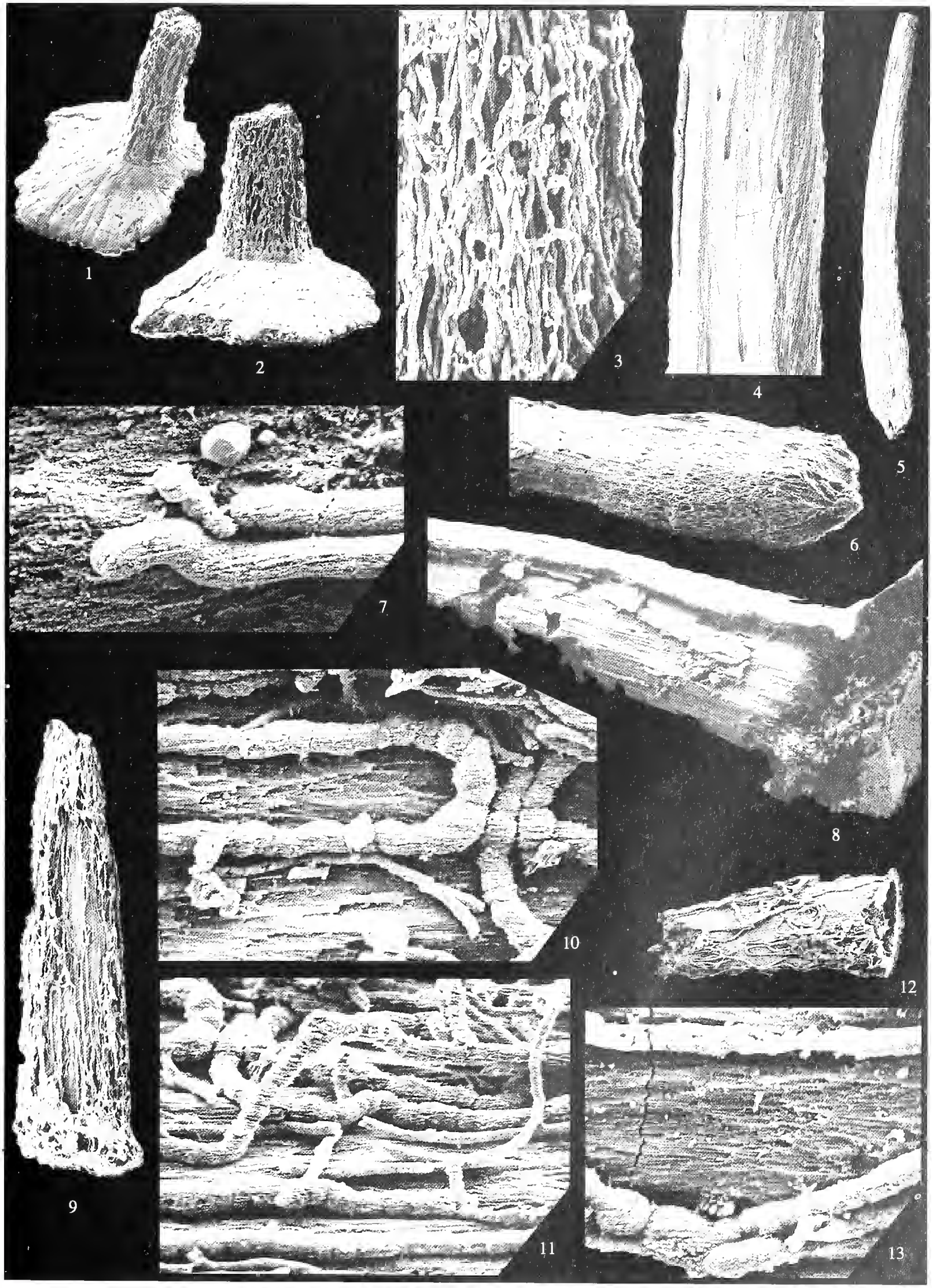
Derivation of generic name. From the Greek *deirados*, meaning ridge, in reference to prominent ridges on both upper and lower surfaces.

Diagnosis. Small sclerites with variably subcircular outline, occasionally tending to quadrate. Dorsal surface bearing tri-radiate ridge, delimiting anterior embayment and paired postero-lateral embayments. Anterior embayment bears transversely elongate spine. Ventral surface bearing tri-radiate ridge in opposite orientation to that of dorsal surface, so delimiting posterior embayment and paired antero-lateral embayments.

EXPLANATION OF PLATE 3

Figs 1–13. *Zhijinites longistriatus* Qian, 1978. 1–3, IGAS-BC-88-30107; 1 and 2, entire sclerite; 3, detail of steinkerns of endolith borings. 4–6, IGAS-BC-88-30108; 4, detail of steinkern surface showing possible replication of wall ultrastructure; 5, steinkern of spine cavity; 6, detail of basal region of steinkern. 7, IGAS-BC-88-30109, detail of steinkerns of endolith borings showing blind terminations and imprint of wall ultrastructure. 8, IGAS-BC-88-30110, steinkern and partial preservation of outer wall. 9–11, IGAS-BC-88-30111; 9, steinkern of spine cavity; 10 and 11, detail of steinkern surface showing wall ultrastructure and endolith borings, note variation in thickness. 12 and 13, IGAS-BC-88-30112; 12, steinkern of spine cavity; 13, detail of steinkern surface showing wall ultrastructure and endolith borings. All isolated sclerites from Bed 36, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications: ×70 (Figs 1, 2, 5, 9, 12); ×500 (Fig. 3); ×350 (Fig. 4); ×140 (Figs 6, 8); ×700 (Figs 7, 10); ×600 (Fig. 11); ×1000 (Fig. 13).

PLATE 3



CONWAY MORRIS and CHEN, *Zhijinites*

Deiradoclavus trigonus gen. et sp. nov.

Plates 4 and 5; Text-fig. 11*c*

Derivation of specific name. On account of the three-angled (*gonia*, Greek for angle) arrangement of the ridges.

Diagnosis. As for the genus.

Holotype. IGAS-BC-88-30114 (Pl. 4, fig. 2).

Paratypes. IGAS-BC-88-30113, 30115–30136.

Stratigraphic horizon. Guojiaba Formation.

Locality. Xuanjiangping section, near Xuanjiangping village, Kuanchuanpu, Shaanxi.

Taxonomic comparisons. With one possible exception, no published descriptions of cambroclaves can be closely compared to *Deiradoclavus*. The exception is specimens from the Yurtus Formation of Xinjiang, referred to *Wuschichites polyedrus* by Qian and Xiao (1984, pl. 3, figs 12 and 13). Here the ventral surface appears to bear a tri-radiate ridge, while the opposite surface is described as having a tri-radiate groove. However, while the tri-radiate pattern recalls *Deiradoclavus*, in this new genus both sides bear ridges. It remains conceivable that *W. polyedrus* should be transferred to *Deiradoclavus*, but synonymy of the genera would not be necessary because of the distinctive status of the type species, *W. minutus* (Qian and Xiao 1984, pl. 1, fig. 7; pl. 3, fig. 11). Although the ventral surface bears a tri-radiate ridge, the sclerites of *W. minutus* differ from *Deiradoclavus* in having a prominent posterior notch and bulbous anterior. Indeed, in the Xinjiang material similar features are also visible in some co-occurring sclerites of *Cambroclavus* (see Qian and Xiao 1984, pl. 3, figs 16, 18, 19); these supposedly distinct sclerites may represent end-members of a single cambroclavid species, so making *Wushichites* a junior synonym of *Cambroclavus* (see Bengtson *et al.* 1990).

Preservation. In common with other cambroclaves, the sclerites of *Deiradoclavus* (Pls 4 and 5) appear to have had their originally calcareous walls replaced and/or partly coated with diagenetic phosphate, leaving the interior of the sclerite hollow. The quality of replication varies, but in some specimens a fibrous arrangement (e.g. Pl. 5, fig. 2) may represent an original ultrastructure of the wall. A similar ultrastructure has been noted in both cambroclaves (Bengtson *et al.* 1990) and zhijinitids (see above).

Description. The sclerites may be sub-circular in outline (Pl. 4, figs 1, 2, 7, 12), but the range of variation is very considerable; many sclerites approach a quadrate shape (Pl. 4, figs 5, 6, 10; Pl. 5, figs 1, 3, 8, 9, 12), while others are relatively elongate (Pl. 4, figs 3 and 4) or more irregular in shape (Pl. 4, figs 12 and 13; Pl. 5, fig. 2). Orientations are based on comparisons with other cambroclaves (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990; see also discussion above of zhijinitid orientation); in particular the spine is taken to be anterior and to arise from the dorsal surface.

Notwithstanding wide morphological variation, the dorsal surface of most sclerites bears a tri-radiate ridge that has a point of divergence located slightly anterior to the mid-line (Pl. 4, figs 1, 2, 10, 11, 13; Pl. 5, figs 1 and 3). The posterior arm, so named because it extends to that margin, is relatively broad and sometimes flares towards its termination. The pair of anterior arms are narrower, and usually diverge from the midline at an angle of about 60°. Variation in development of these ridges, however, is considerable. In some specimens the

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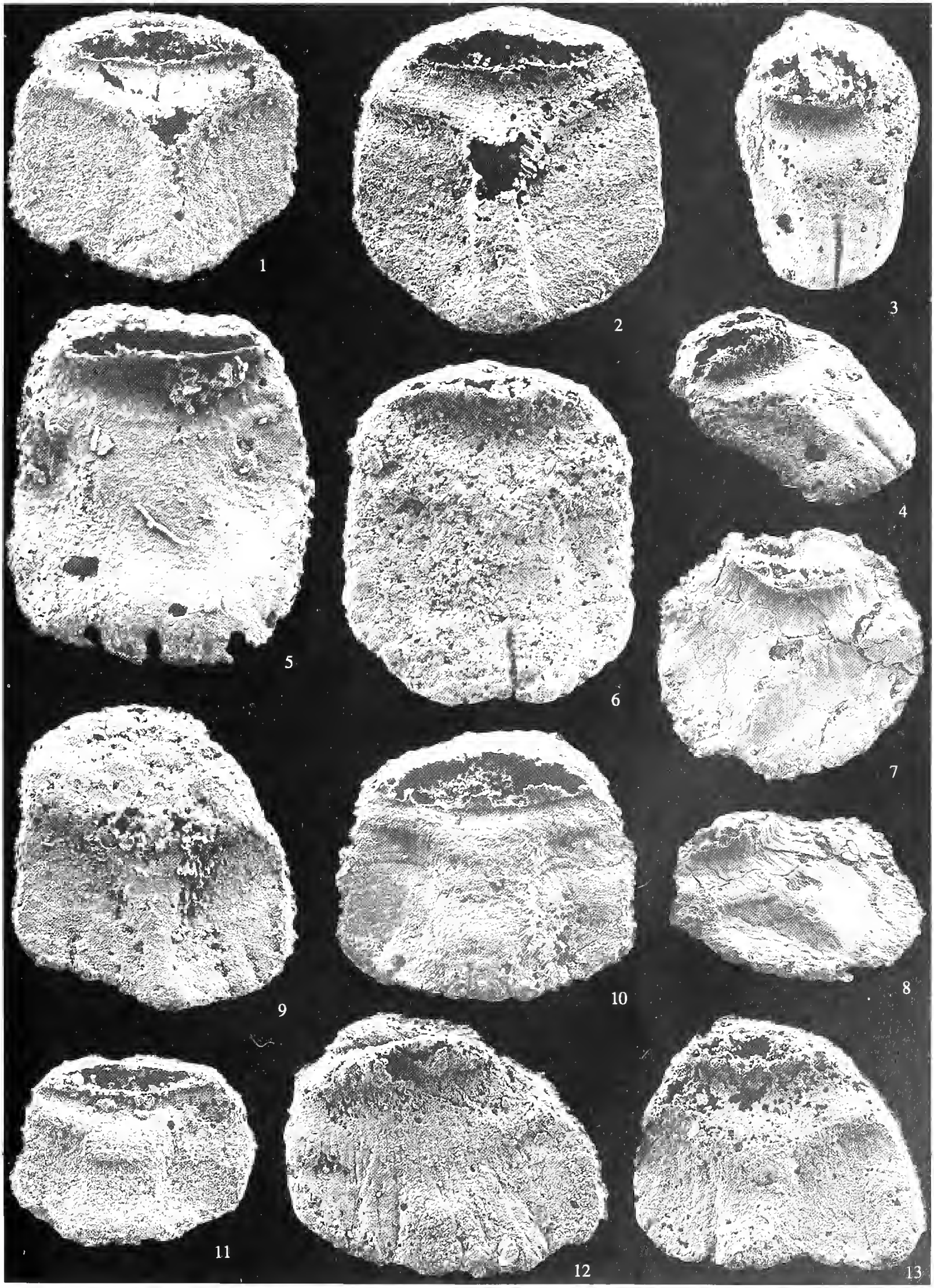
EXPLANATION OF PLATE 4

Figs 1–13. *Deiradoclavus trigonus* gen. et sp. nov. 1, IGAS-BC-88-30113. 2, IGAS-BC-88-30114, holotype. 3 and 4, IGAS-BC-88-30115. 5, IGAS-BC-88-30116. 6, IGAS-BC-88-30117. 7 and 8, IGAS-BC-88-30118. 9, IGAS-BC-88-30119. 10, IGAS-BC-88-30120. 11, IGAS-BC-88-30121. 12, IGAS-BC-88-30122. 13, IGAS-BC-88-30123. All isolated sclerites, dorsal surface, from the Guojiaba Formation at Xuanjiangping section near Kuanchuanpu, Shaanxi, China. Magnifications all ×90.

PLATE 4



CONWAY MORRIS and CHEN, *Deiradoclavus*

posterior arm is very broad and may bear either a median furrow (Pl. 4, figs 3 and 4; Pl. 5, fig. 3) or a series of grooves (Pl. 4, figs 10 and 12) that are irregularly disposed and extend from the posterior margin by variable amounts. Similarly, the strength of development of the anterior arms varies, but usually at least some trace is perceptible (Pl. 4, fig. 5). The tri-radiate nature of the ridge defines three gently concave depressions, termed here embayments, that open towards the anterior margin (1) and postero-lateral margins (2, 3) respectively. The anterior embayment houses a narrow, transversely elongate ridge (Pl. 4; Pl. 5, figs 1–3) whose distal termination is not known owing to incomplete phosphatization. This structure is referred to as the anterior spine, a term that, while not precisely descriptive, emphasizes its presumed homology with comparable structures in other cambroclaves.

The ventral surface also bears a tri-radiate ridge (Pl. 5, figs 4–15), although its sense of branching is reversed (i.e. rotated through 180°), in comparison to the Y-shaped ridge on the upper surface. Accordingly, an anterior ridge diverges from the paired postero-lateral ridges, with the point of divergence located more or less at the mid-point of the sclerite. Although the anterior arm is sometimes a single crest, more often it forms a pair of ridges that are separated by a median depression (Pl. 5, figs 4–6, 14). On occasions this furrow is bisected by yet another ridge (Pl. 5, figs 10 and 11). The postero-lateral arms are usually simple and diverge at an angle that is controlled by the shape of the sclerite and varies from about 125°, in sclerites which are broader than long (Pl. 5, fig. 5), to about 100° where the sclerite is more quadrate (Pl. 5, fig. 12). The embayments defined by the tri-radiate ridge on the ventral surface are broadly concave. This is particularly noticeable in the posterior embayment (Pl. 5, figs 4, 11, 13) that is flanked by the postero-lateral arms. The anterior embayments occasionally bear subsidiary ridges (Pl. 5, figs 10 and 11) and may also be traversed by subdued grooves (Pl. 5, fig. 15).

Palaeoecology. Evidence from fused sclerites (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990), articulatory facets, and outline shapes that allow for mutual accommodation and interlocking in *Cambroclavus* all suggest that the animal was originally coated by a scleritome (Text-fig. 11*b*). Fused sclerites have not been recognized in *Deiradoclavus*, but the paired postero-lateral embayments on the dorsal surface are interpreted as acting as points of articulation with the anterior corners of the two adjacent sclerites (Text-fig. 11*c*). In this schema the anterior depression, defined by the two ridges on the ventral surface of most sclerites, would act to accommodate the posterior arm on the dorsal surface of the next sclerite to the anterior. Such an interlocking pattern would have provided a more or less continuous cover of the body, providing an effective armour, especially with the added complement of spines projecting from the anterior of each sclerite.

Relationships. *Deiradoclavus trigonus* is regarded as a cambroclave because of its broad similarity to *Cambroclavus* spp, including an anterior spine and median ridge flanked by embayments. Indeed, rare sclerites approach quite closely *Cambroclavus* (Pl. 4, figs 3 and 4), but the great majority differ in three principal ways: they are more or less sub-circular to quadrate rather than elongate, they bear prominent tri-radiate ridges on both dorsal and ventral surfaces, and the anterior spine is elongately transverse rather than a simple conical extension.

Mention was made above concerning possible comparisons between *Deiradoclavus* and *Wushichites*, especially *W. polyedrus* (Qian and Xiao 1984). With the available illustrations and lack of information on scleritome variability of co-occurring cambroclaves, objective comparisons are not easy, and the possible inclusion of *W. polyedrus* in *Deiradoclavus* must be regarded as tentative. Although *Zhijinites* has a more or less circular base, it is surmounted by an eccentrically located spine and is less similar to *Deiradoclavus* than *Cambroclavus*. Indeed the transition between

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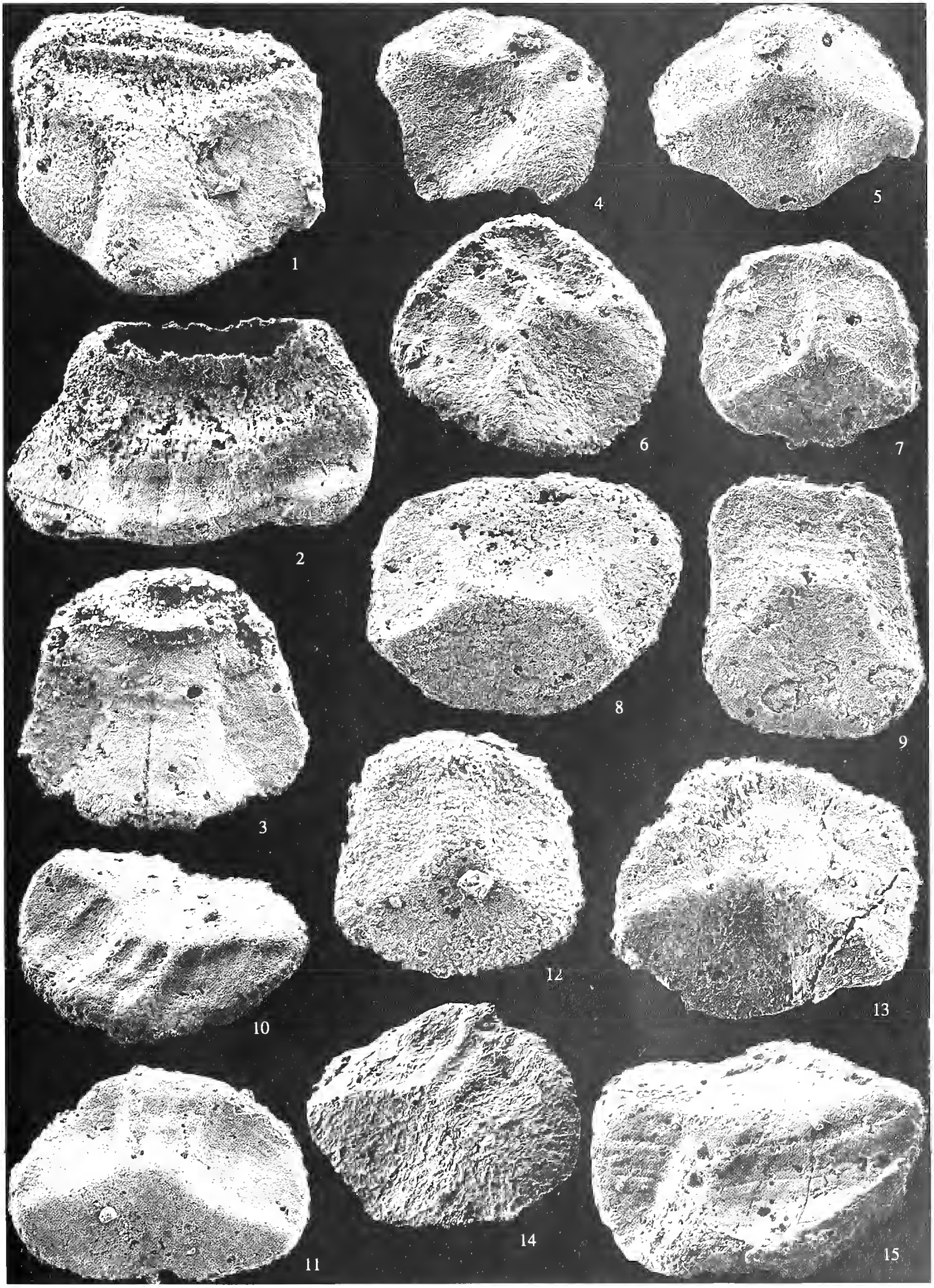
EXPLANATION OF PLATE 5

Figs 1–15. *Deiradoclavus trigonus* gen. et sp. nov. 1, IGAS-BC-88-30124. 2, IGAS-BC-88-30125. 3, IGAS-BC-88-30126. 4 and 5, IGAS-BC-88-30127. 6, IGAS-BC-88-30128. 7, IGAS-BC-88-30129. 8, IGAS-BC-88-30130. 9, IGAS-BC-88-30131. 10 and 11, IGAS-BC-88-30132. 12, IGAS-BC-88-30133. 13, IGAS-BC-88-30134. 14, IGAS-BC-88-30135. 15, IGAS-BC-88-30136. All isolated sclerites, dorsal (Figs 1–3) and ventral (Figs 4–15) surfaces, from Guojiaba Formation at Xuanjiangping section near Kuanchuanpu, Shaanxi, China. Magnifications all ×90.

PLATE 5



CONWAY MORRIS and CHEN, *Deiradoclavus*

Zhijinites and *Cambroclavus* may be envisaged as arising from an extension of the posterior region and the development of a closely interlocking scleritome. *Deiradoclavus* would be derived in turn from a cambroclavid by decreasing the length to width ratio, which would also explain the transversely elongate spine.

Genus DELTACLAVUS gen. nov.

Type species. Deltaclavus graneus gen. et sp. nov.

Derivation of the generic name. On account of the triangular or delta shape of the sclerites.

Diagnosis. Sclerites with broad anterior edge, and lateral edges converging to posterior point, imparting triangular outline. Dorsal surface with longitudinal median ridge, terminating anteriorly in subdued spine. Lateral portions of dorsal surface gently concave. Ventral surface with prominent anterior facet, sometimes bounded by subdued ridges. Remainder of ventral surface gently rounded and more or less smooth.

Deltaclavus graneus sp. nov.

Plates 6 and 7; Text-figs 8, 9, 11*d*

Derivation of specific name. From the Latin *graneus*, in reference to the seed or pip-like appearance of the individual sclerites.

Diagnosis. As for the genus.

Holotype. IGAS-BC-88-30180 (Text-fig. 9*a–c*).

Paratypes. IGAS-BC-88-30154-30179, 30181.

Stratigraphic horizon. Lower Shuijingtuo Formation, Lower Cambrian.

Locality. Taishanmiao section, near the village of Taishanmiao, Hubei.

Preservation. The style of preservation, with secondary phosphatization of the sclerite wall and limited infill of the central cavity, is comparable to that described above for the type material of *Deiradoclavus trigonus* gen. et sp. nov.

Description. The majority of specimens are isolated sclerites (Pls 6 and 7), but rare examples of fused assemblages (Text-figs 8 and 9) are of considerable importance for partial scleritome reconstruction. In comparison with other cambroclave species, isolated sclerites are relatively small, typically about 350–400 μm in length. In dorso-ventral view the sclerites have a triangular shape, defined by a gently convex arcuate anterior margin and lateral margins that converge posteriorly to a pointed termination (Pl. 6, figs 1, 4, 5, 7, 11, 14; Pl. 7, figs 1, 5, 6, 8, 11, 13). The outline shape varies from relatively narrow (Pl. 6, fig. 5) to rarer broader sclerites (Pl. 6, fig. 13; Pl. 7, figs 3 and 8). In lateral view, the sclerite is highest at the anterior, and declines posteriorly (Pl. 6, figs 3, 6, 12, 13; Pl. 7, figs 2 and 3). The dorsal surface bears a prominent median ridge that at the anterior end expands into a broader area, surmounted by a knobbly spine (Pl. 6, figs 1, 8, 14; Pl. 7, figs 1 and 4). In narrower sclerites this latter structure is more or less circular, but in broader ones it is transversely

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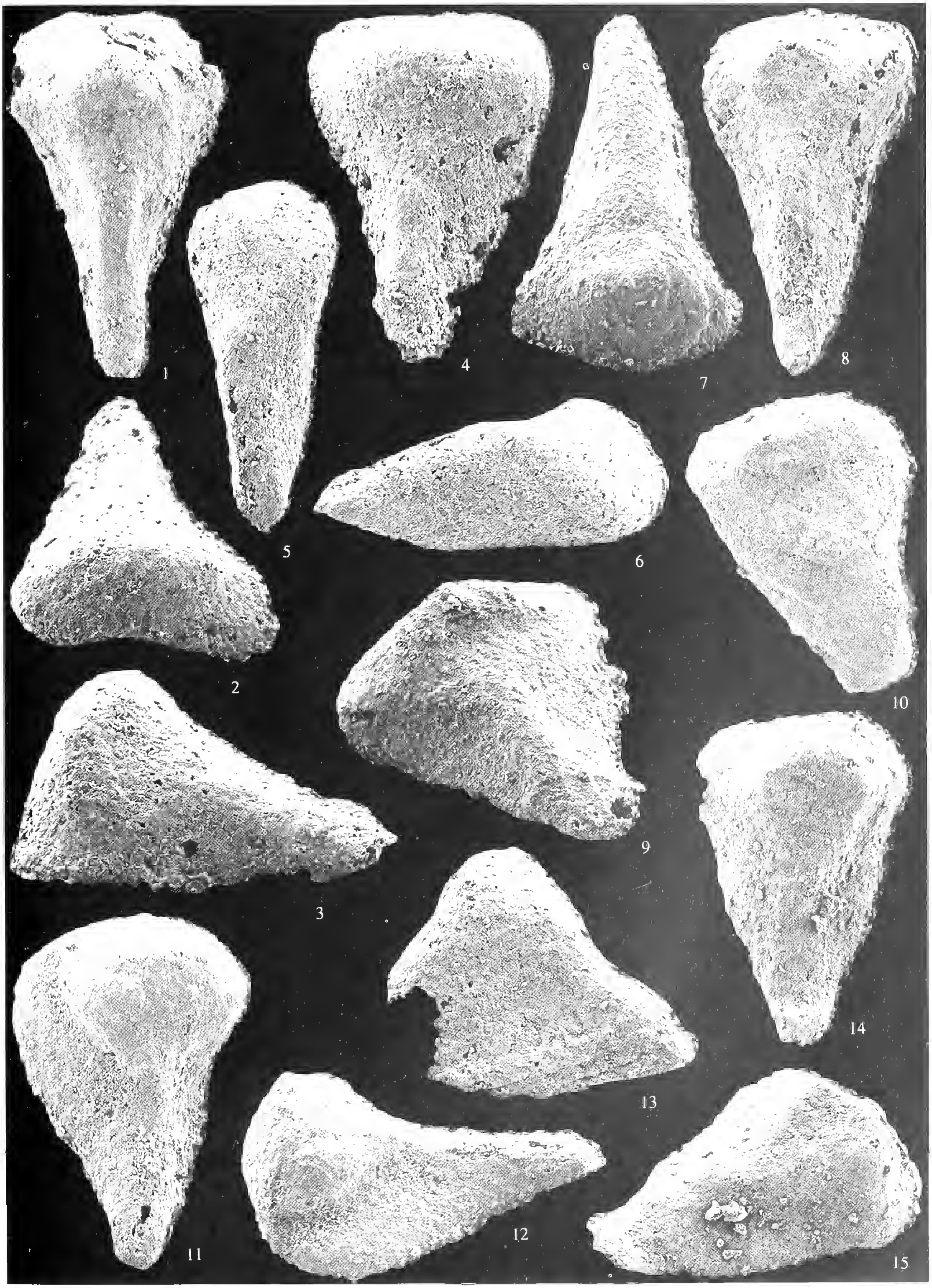
EXPLANATION OF PLATE 6

Figs 1–15. *Deltaclavus graneus* gen. et sp. nov. 1, IGAS-BC-88-30154. 2–4, IGAS-BC-88-30155. 5 and 6, IGAS-BC-88-30156. 7, IGAS-BC-88-30157. 8, IGAS-BC-88-30158. 9, IGAS-BC-88-30159. 10, IGAS-BC-88-30160. 11 and 12, IGAS-BC-88-30161. 13, IGAS-BC-88-30162. 14 and 15, IGAS-BC-88-30163. All isolated sclerites, dorsal surface, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications all × 150.

PLATE 6



CONWAY MORRIS and CHEN, *Deltaclavus*

expanded. Although this projection is more nodose than spinose, the term spine is employed here (as with *Deiradoclavus trigonus* gen. et sp. nov., see above) because of its inferred homology with other cambroclavid spines. The lateral regions on either side of the dorsal ridge are gently concave. Apart from occasional sclerites with subdued ridge-like developments, the dorsal surface is more or less smooth. The ventral surface is also more or less smooth, and gently rounded, except at the anterior end where there is a distinct concave facet that may be flanked by subdued ridges (Pl. 7, figs 6–14).

Fused assemblages of sclerites occur as two variants. The first type consists of a longitudinal file of three, four or five sclerites with the posterior dorsal surface in juxtaposition to the ventral facet of the anterior region (Text-figs 8*a*, *b* and 9*a*–*c*). The second variant consists of fused rows, that also articulate via their ventral surface with another row such that the posterior ends of opposite sclerites touch one another. Two such examples of sclerite rows running 'back to back' have been recognized. One consists of a single file (Text-fig. 8*c*–*f*) on each side, and the other of a double file (Text-fig. 9*d*–*h*). In the latter case the interlocking of adjacent sclerites of each file on either side is seen to alternate. The sclerites of the second type of fused assemblage are broader, with the posterior termination more distinctly demarcated from the remainder of the sclerite whose lateral edges tend to be wing-like.

Remarks. The significance of the fused assemblages of *D. graneus* in scleritome reconstruction of cambroclaves is discussed below. Specimens of sclerites comparable to *Deltaclavus* appear not to have been recognized previously, although in this context attention should be drawn to problematical fossils from the Lower Tal Formation of Uttar Pradesh, India. In particular a specimen illustrated by Bhatt *et al*. (1983, pl. 2, fig. 2) seems to be comparable to *D. graneus*, and in any event their attribution to *Sachites* seems unlikely. It should be noted that the stratigraphic position of the Indian occurrence at present is correlated with substantially older sequences (Brasier and Singh 1987) than the Shuijingtuo Formation from which *D. graneus* derives.

Family PARACARINACHITIDAE Qian, 1984

Diagnosis (emended from Qian 1984). Sclerites concavo–convex, more or less bilaterally symmetrical. Elongate spatula-like axis, tapering to blunt apex, usually bearing median row of spines but sometimes smooth. Lateral flanges, wing-like, sometimes present, smooth except for occasional furrows. Incremental growth. Calcareous composition.

Discussion. Qian and Bengtson (1989, p. 48) only referred to this family in passing, but noted that *Paracarinachites* might be related to *Scoponodus* Jiang, 1982. They drew attention to possible similarities to *Ernogia* Jiang, 1982, and as noted below it may transpire that both these genera should be accommodated in Paracarinachitidae.

PARACARINACHITES Qian and Jiang, 1982

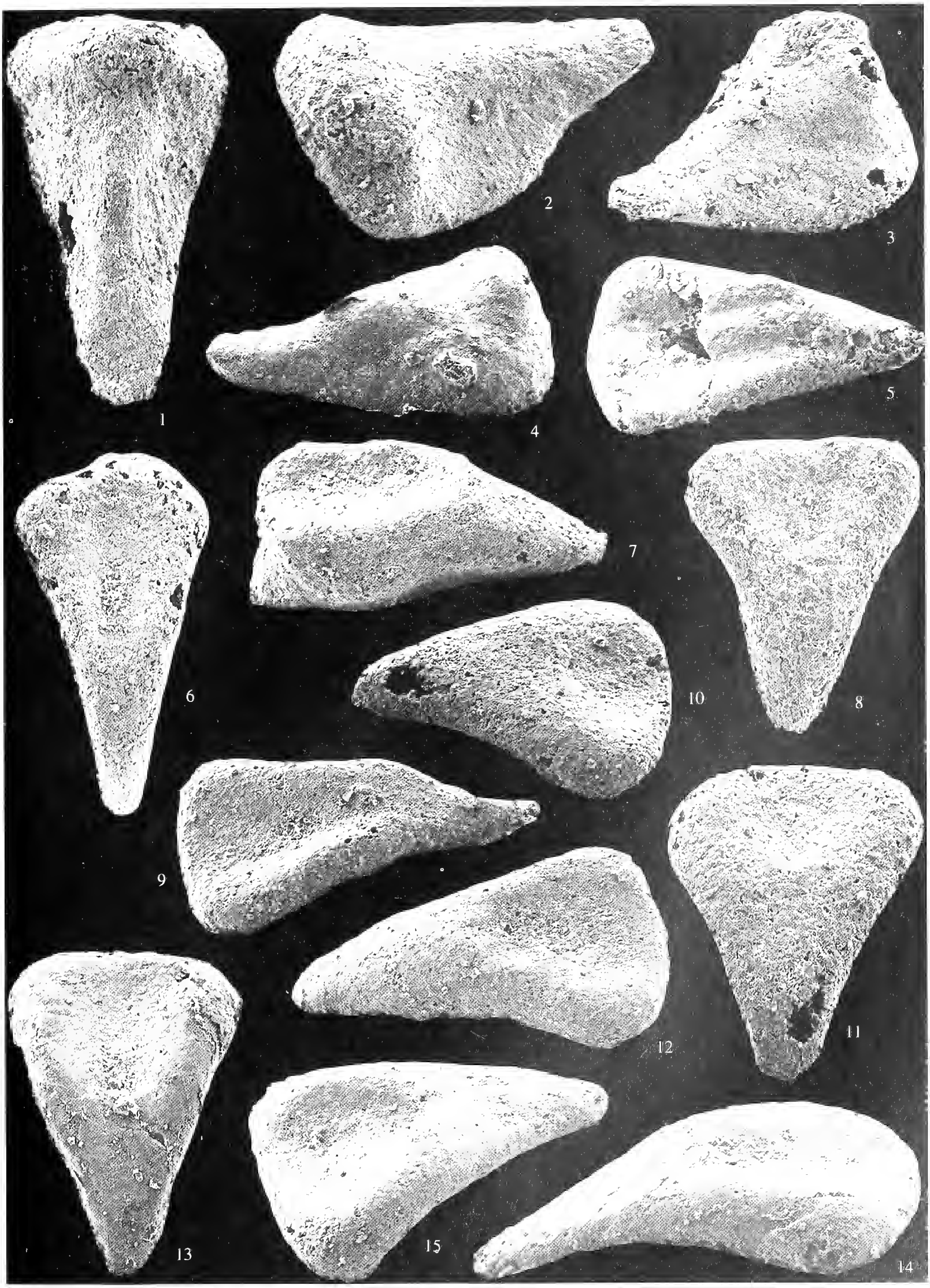
Type species. *Paracarinachites sinensis* Qian and Jiang, 1982.

Diagnosis. See Qian and Bengtson (1989, p. 49).

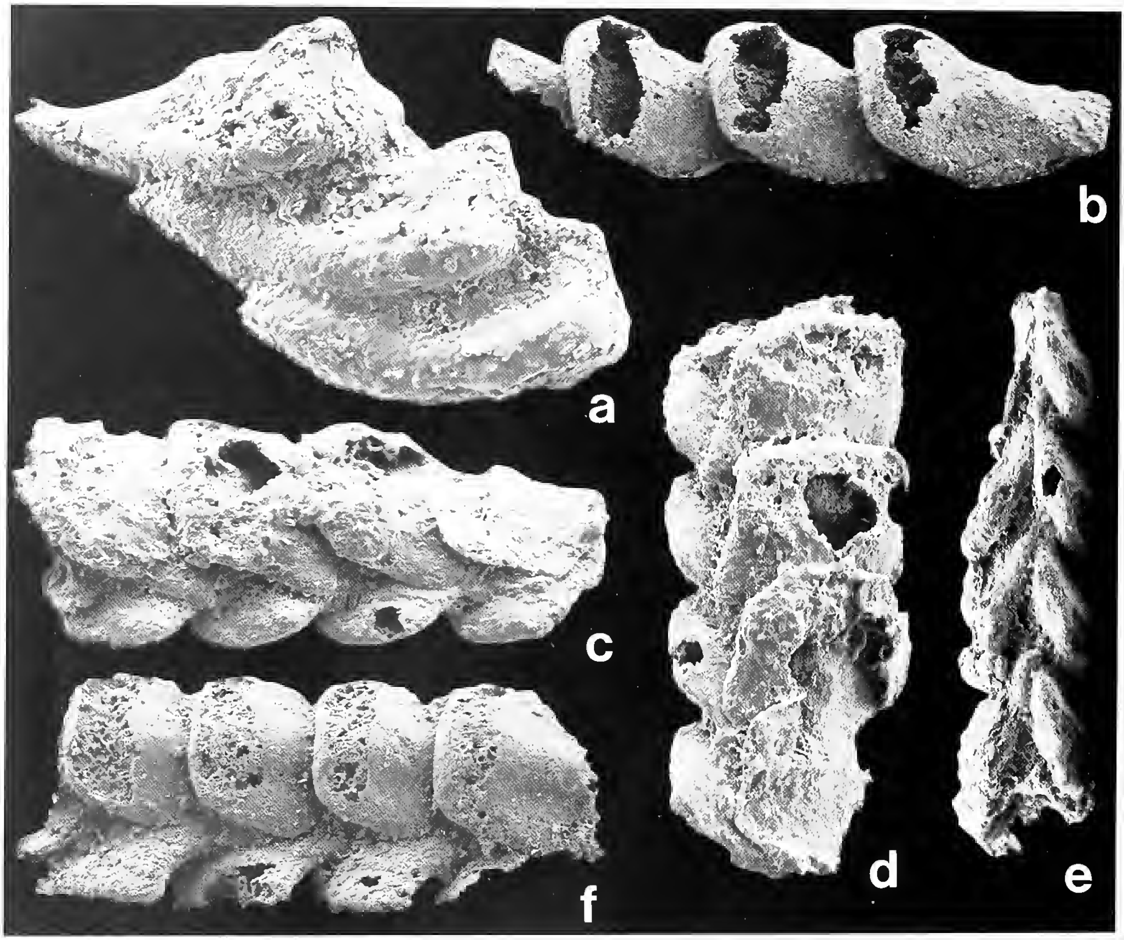
EXPLANATION OF PLATE 7

Figs 1–15. *Deltaclavus graneus* gen. et sp. nov. 1, IGAS-BC-88-30164. 2, IGAS-BC-88-30165. 3, IGAS-BC-88-30166. 4, IGAS-BC-88-30167. 5, IGAS-BC-88-30168. 6, IGAS-BC-88-30169. 7, IGAS-BC-88-30170. 8, IGAS-BC-88-30171. 9, IGAS-BC-88-30172. 10 and 11, IGAS-BC-88-30173. 12, IGAS-BC-88-30174. 13 and 14, IGAS-BC-88-30175. 15, IGAS-BC-88-30176. All isolated sclerites, dorsal (Figs 1–4) and ventral (Figs 5–15) surfaces, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications all × 150.

PLATE 7



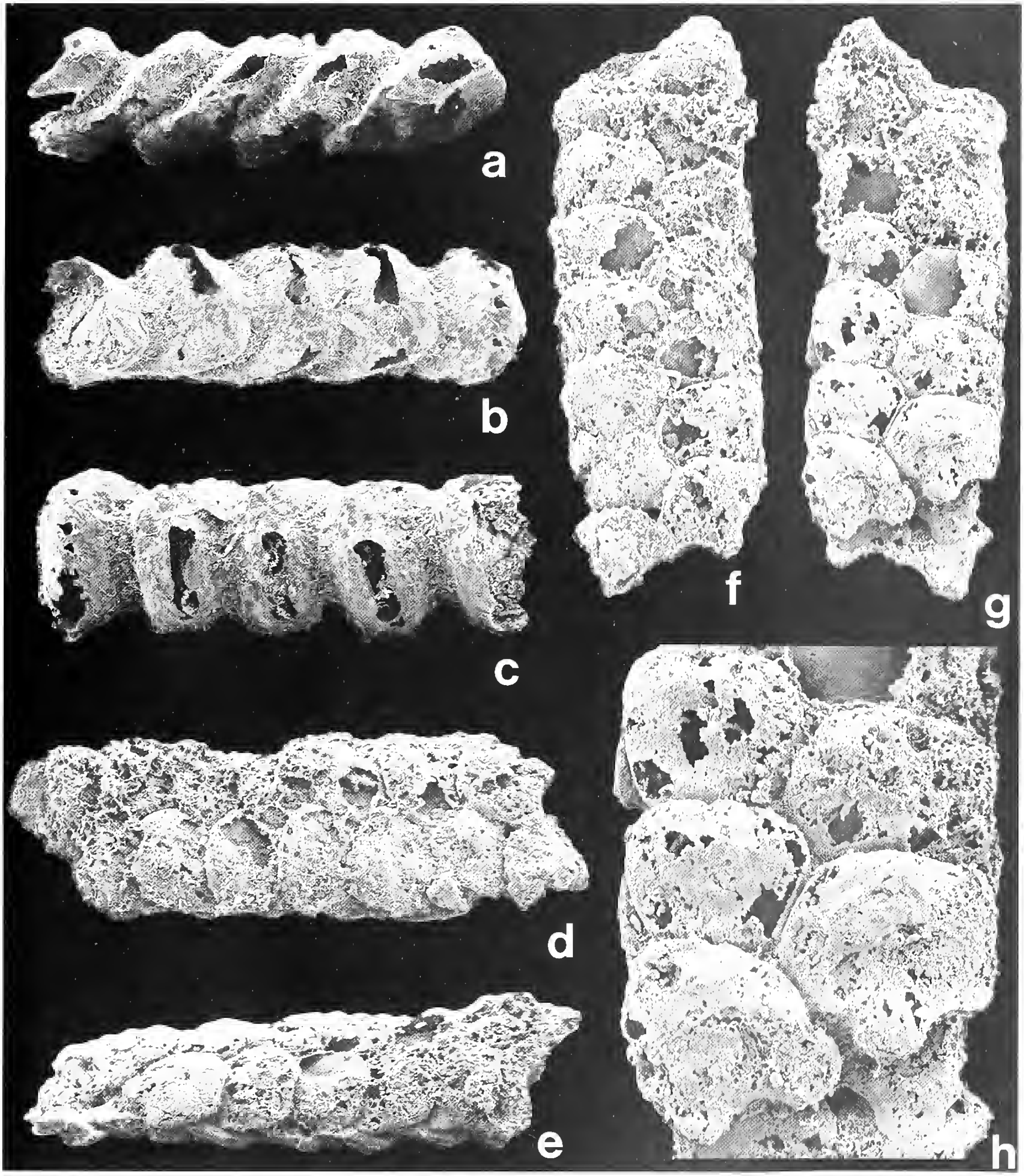
CONWAY MORRIS and CHEN, *Deltaclavus*



TEXT-FIG. 8. *Deltaclavus graneus* gen. et sp. nov. *a*, IGAS-BC-88-30177. *b*, IGAS-BC-88-30178. *c–f*, IGAS-BC-88-30179; *c* and *d*, 'lower' surface; *e*, lateral view; *f*, 'upper' surface. All articulated series of sclerites, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications: *a*, × 150; *b–f*, × 100.

Discussion. An extensive discussion of *Paracarinachites* (junior synonyms include *Yangtzechiton* Yu 1984*a*, *Luyanhaochiton* Yu 1984*a*) is provided by Qian and Bengtson (1989) who recognised four species (*P. sinensis*, *P. columellatus*, *P. parabolicus* and *P. spinus*; whether the species erected by He and Xie (1989, pl. 1, figs 13–15) as *Paracarinachites bispinosus* can be included in this genus seems to be more questionable). In each case the available specimens consist of elongate, bilaterally symmetrical sclerites composed of a series of growth increments that are usually marked by denticles arising from the outer side. In *P. spinus* the incremental nature of the sclerites is particularly clear on account of the prominent divisions that convey the impression of units overlapping in an abapical direction (see Qian and Bengtson 1989, fig. 29; He and Xie 1989, pl. 1, figs 17–19, 21). Qian and Bengtson (1989) emphasized, however, that the sclerite was a single unit, citing evidence of lateral fusion on the outer side and a seamless appearance on the lower side that they interpreted as resulting from the adpression of successive lamellae during growth.

Here we report also zhijinitid-like denticles that are strikingly similar to the increments that go to make up the sclerites of *P. spinus* as reported by Qian and Bengtson (1989; see also He and Xie



TEXT-FIG. 9. *Deltaclavus graneus* gen. et sp. nov. *a–c*, IGAS-BC-88-30180, holotype; *a*, lateral view; *b*, oblique view; *c*, dorsal view. *d–h*, IGAS-BC-88-30181; *d*, *f*, 'lower' surface; *e*, *g*, 'upper' surface; *h*, detail of 'upper' surface. All articulated series of sclerites, from the Shuijingtou Formation at the Taishanmiao section, near Taishanmiao, Hubei, China. Magnifications: *a–c*, × 100; *d–g*, × 75; *h*, × 150.

1989). The recognition of separate elements need not negate Qian and Bengtson's interpretation of an incremental assemblage and the significance of these observations on the affinities of *Paracarinachites* are returned to below.

Paracarinachites spinus (Yu, 1984*a*)

Plate 8; Text-fig. 10

Diagnosis. For isolated sclerites: base semi-circular to oval with concave ventral surface, dorsal surface bearing prominent curved spine, inserted towards anterior side. Dorsal surface variously ornamented, including concentric ridge and towards margin radial ridges. For fused sclerites, see Qian and Bengtson (1989).

Holotype. ASN 84135 (see Yu 1984*a*, pl. 1, figs 8 and 9).

Material illustrated here. IGAS-BC-88-30137–30153.

Remarks. A synonymy and discussion of the taxonomic status of these sclerites are provided by Qian and Bengtson (1989), to which may be added illustrations of fused and isolated sclerites from Meishucun by He and Xie (1989, pl. 1, figs 16–22) who continued to refer to it as *Yangtzechiton elongatus*. In addition, it seems conceivable that one specimen identified as *Zhijinites* sp. from the top of the Zhongyicun Member at Meishucun (Jiang 1980, pl. 4, fig. 17; the other specimen illustrated in pl. 4, fig. 18 may not be a cambroclave) is an isolated sclerite comparable to material described here. The status of *Z. undulatus* in this context is more uncertain. One sclerite, from near Leibo, Sichuan (Jiang 1982, pl. 17, fig. 12, 12*a*) might be tentatively referred to *P. spinus*. However, the other specimens illustrated by Jiang (1982, pl. 17, fig. 11), from the Dahai section near Huize, are assigned provisionally to *Z. longistriatus* (see above).

Stratigraphic horizon. Bed 7, Zhongyicun Member, Yuhucun Formation, Meishucun Stage, Lower Cambrian.

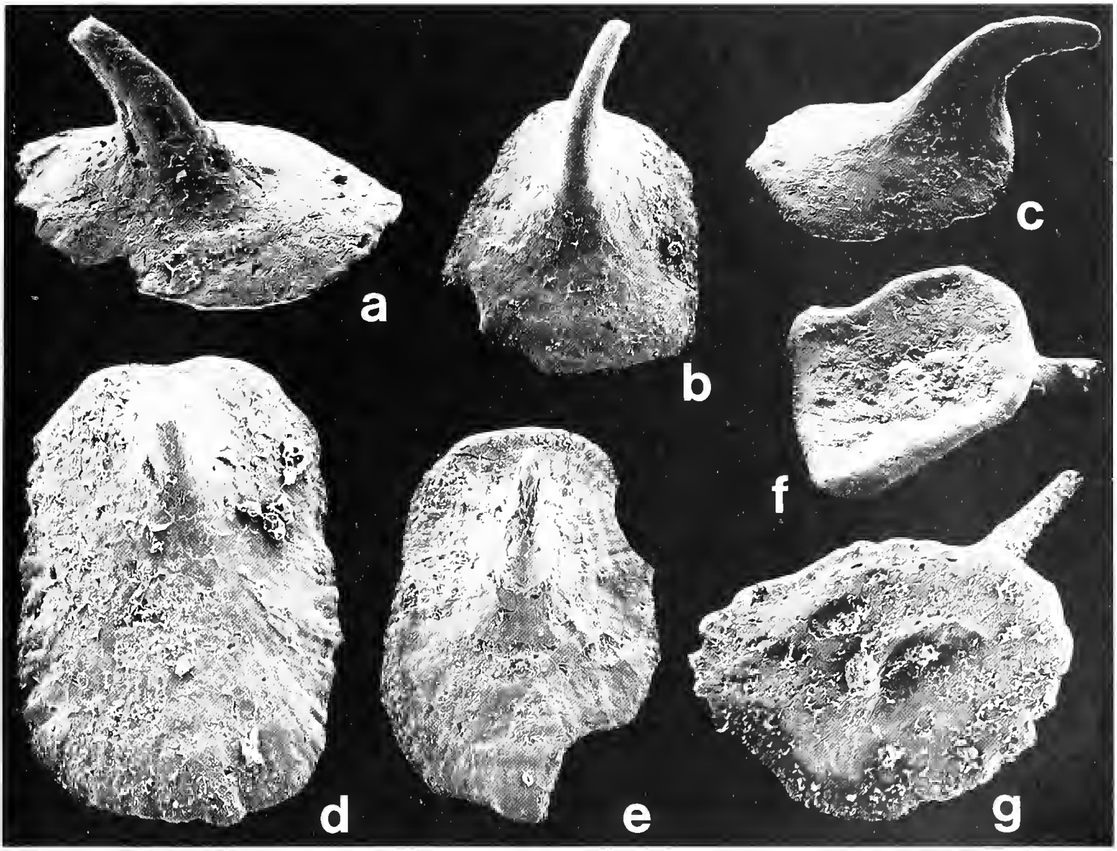
Locality. Xiaowaitoushan section, Kunyang Phosphorite Mine, Meishucun, Yunnan.

Preservation. The sclerites are replaced with massive phosphate, which in etched and polished material is seen to replace not only the walls but also the internal cavity.

Description. The sclerites are divisible into a sub-circular to oval base and elongate spine (Pl. 8; Text-fig. 10). The former unit has a concave lower surface, that is more or less smooth (Pl. 8, fig. 6; Text-fig. 10*f*, *g*). The opposite surface of the base usually bears subdued ornamentation, which may include a series of concentric ridges (Pl. 8, figs 2, 3, 17; Text-fig. 10*e*) or more occasionally a more pronounced furrow (Pl. 8, figs 14 and 15). A finer-scale ornamentation of radial ridges, that tends to be most accentuated near the margins, is characteristic (Pl. 8, figs 1, 4, 5, 7, 8, 10, 15, 17; Text-fig. 10*e*). The margins themselves are often more or less smooth, but on occasion they show indentations or more developed scallops, especially on the posterior margin.

The spine is conspicuous, usually stout, and terminates in a simple point. Its insertion is eccentric, towards the presumed anterior side and it may even arise from the anterior margin (Text-fig. 10*c*). The degree of curvature is variable, and although in most sclerites the spine inclines towards the posterior mid-point, in some specimens the spine is recurved to one side (Text-fig. 10*b*).

Discussion. If a series of these sclerites was aligned in an imbricated file parallel to their antero-posterior axes they would appear to be almost indistinguishable from the fused assemblages described by earlier workers (Qian and Bengtson 1989; see also Yu 1984*a*, *b*, 1989). Qian and Bengtson (1989) presented evidence for the fused assemblages to be primary rather than diagenetic, although in either case juxtaposition of the sclerites presumably reflects a life orientation. Unless the fused assemblages are teratological, then it seems likely that they derived from one or more specific



TEXT-FIG. 10. *Paracarinachites spinus* (Yu, 1984). *a*, IGAS-BC-88-30148. *b* and *c*, IGAS-BC-88-30149. *d*, IGAS-BC-88-30150. *e*, IGAS-BC-88-30151. *f*, IGAS-BC-88-30152. *g*, IGAS-BC-88-30153. All isolated sclerites, dorsal (*a–e*) and ventral (*f* and *g*) surfaces, from Bed 7, Zhongyicun Member, Yuhucun Formation at Xiaowaitoushan section, Kunyang Phosphorite Mine, Meishucun, Yunnan, China. Magnifications all ×90.

regions of the body, while the isolated sclerites described here (see also He and Xie 1989) come from other regions.

Apart from occurrences of fused assemblage of *Paracarinachites spinus*, the sclerites of this taxon differ from those of *Zhijinites longistriatus* in several respects. These include relative proportions of base to spine, and ornamentation of spine. However, as noted below, *P. spinus* may be considerably more closely related to the zhijinitids (see also Qian and Bengtson 1989, p. 56) than other species of *Paracarinachites* (including the type species, *P. sinensis*), so that inclusion in the Zhijinitidae may be a preferred option. If this transpires to be the case then the similarity between the serial row of fused sclerites in *P. spinus* and the spinose row in other paracarinachitids would be convergent.

Protopterygotheca leshanensis Chen in Qian, Chen and Chen, 1979

Plate 9; Text-figs 12 and 13

1977 *Protopterygotheca leshanensis* (nomen nudum) Zhong [Chen], p. 122, pl. 3, figs 16–18.
1979 *Protopterygotheca leshanensis* Chen in Qian *et al.*, pp. 221–222, pl. 3, figs 18 and 19.

Discussion. Although fossils attributable to this taxon were illustrated by Zhong [Chen] (1977), the formalities necessary for a proper description were not met until 1979 (Qian *et al.* 1979) when

Protopterygotheca leshanensis became a valid taxon. As noted below several species of *Solenotia* may also be compared to *Protopterygotheca*.

Diagnosis. Sclerite broadly trilobate with elongate central axis flanked by marginal flanges. Strongly convex axis, apex bluntly pointed and increasing width abapically. Axis usually smooth, but occasionally with transverse furrows, and more rarely subdued denticles in median row. Lateral zones slope from axis, outline more or less triangular. Lateral zones usually smooth, but may bear transverse or more occasionally longitudinal folds. Sclerite edges marked by doublure, sometimes showing growth increments. Interior of sclerite usually smooth, occasionally irregular furrows on marginal zone.

Holotype. ASN 51764.

Paratypes. IGAS-BC-88-30183-30198.

Stratigraphic horizon. Beds 36 and 37, Maidiping Member, Hongchunping Formation, Meishucun Stage, Lower Cambrian (see also Zhong [Chen] 1977; note that the holotype is recorded as coming from the Tianzhushan section, near Yichang, Hubei (see Qian *et al.* 1979, p. 222)).

Locality. Maidiping section, Emei, Sichuan.

Preservation. The sclerites are preserved as fine-grained phosphate, densely interwoven with abundant vermiform tubules (Pl. 9, fig. 15). This texture appears to have resulted by diagenetic phosphatization, possibly of an originally calcareous skeleton. The tubules are believed to represent endolithic organisms, possibly algae, that infested disassociated sclerites after the death of the animal.

Description. Sclerites show wide morphological variability about a basic deltoid shape that consists of a central axis flanked by marginal zones (Pl. 9, figs 1, 2, 4–14; Text-fig. 12*a*, *b*, *d*, *g*, *h*). Sclerites appear to have been more or less bilaterally symmetrical, although differences in outline and furrow development on each lateral zone leads to slight departures in symmetry. The sclerites are orientated with respect to the beak-like apex of the central axis, arbitrarily regarded as anterior, and the convex dorsal surface being distinguished from the corresponding concave ventral surface.

The central axis is strongly convex. Its angle of cross-section may exceed 180°, so that the furrow between the axis and lateral flanges forms a recessed overhang (Text-fig. 12*g*). The axis tapers anteriorly to a blunt apex, while its expansion in the opposite direction is relatively even (Pl. 9, figs 1, 5–8, 11; Text-fig. 12*h*). The posterior edge may be largely occupied by this expanded central axis, which tends to have a more flattened convexity than adapically. In longitudinal section the axis tends to be gently arcuate about a mid-point, with both anterior and posterior sections curving downwards (Pl. 9, fig. 4; Text-fig. 12*d*, *i*). In most sclerites the central axis is more or less smooth. More occasionally, especially when the axis is relatively broad, it is traversed by furrows (Pl. 9, fig. 13). These are relatively subdued, and while some are irregularly developed others can be traced across the entire axis and on the midline form an anterior cuspate extension. In such cases the midline also bears an associated series of subdued tubercles inclined abapically (Text-fig. 12*e*, *f*).

The extent of the lateral flanges appears to be controlled in part by preservation, but also reflects original variation. The angle the flanges make with the axial zone varies widely so they may be more or less flat or contribute significantly to the overall convexity of the sclerite. Along the anterior edges the lateral extension

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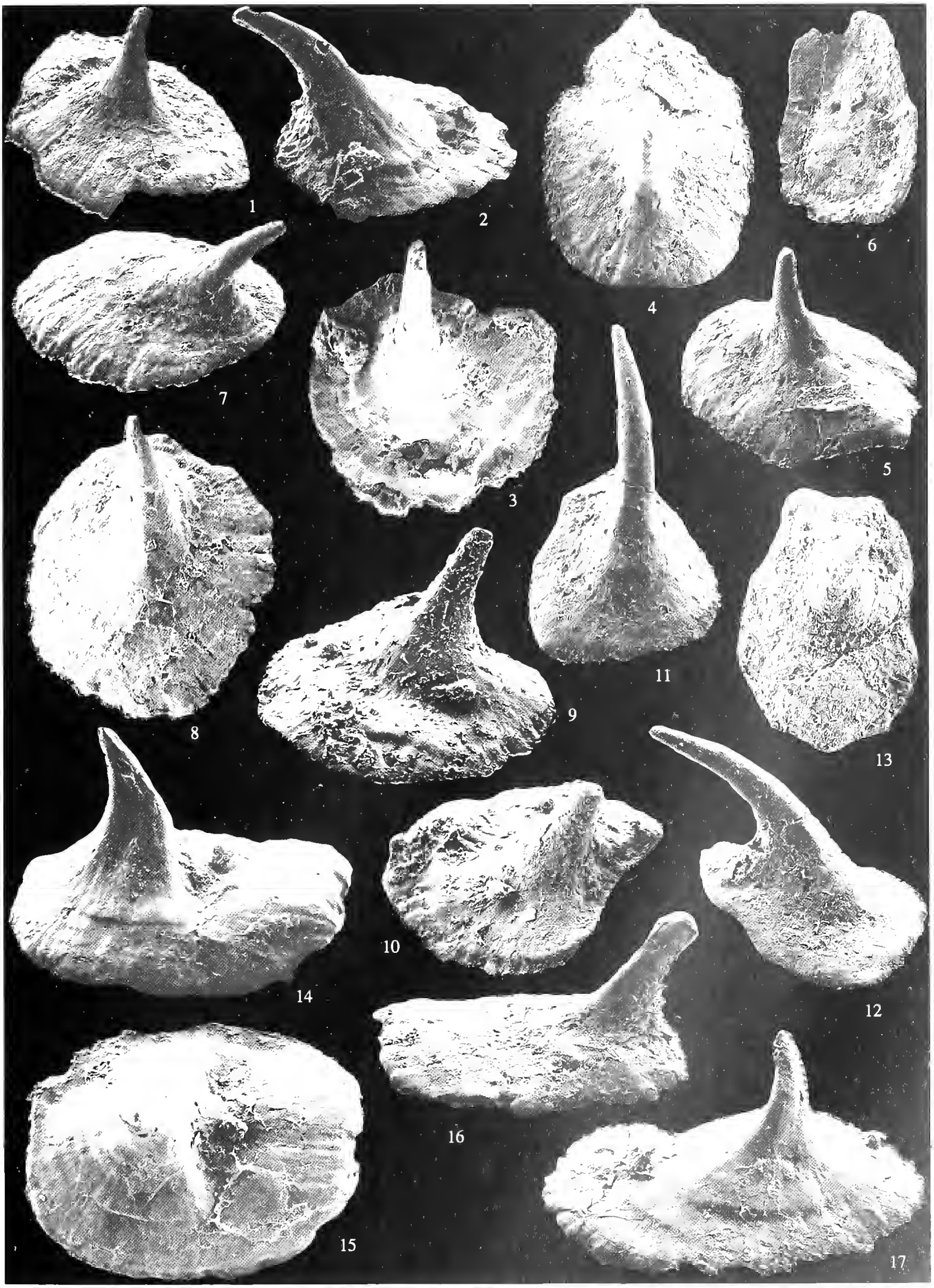
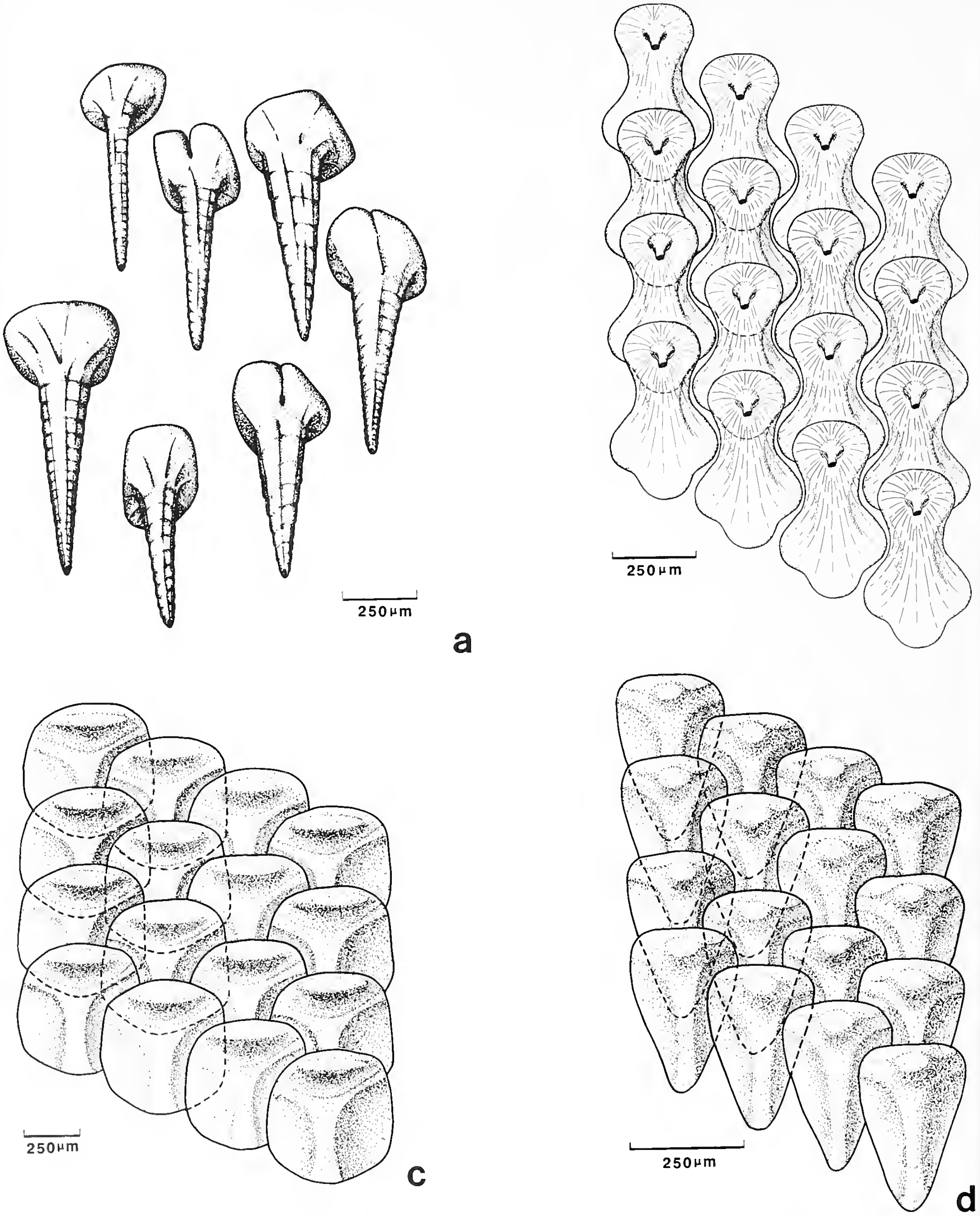
EXPLANATION OF PLATE 8

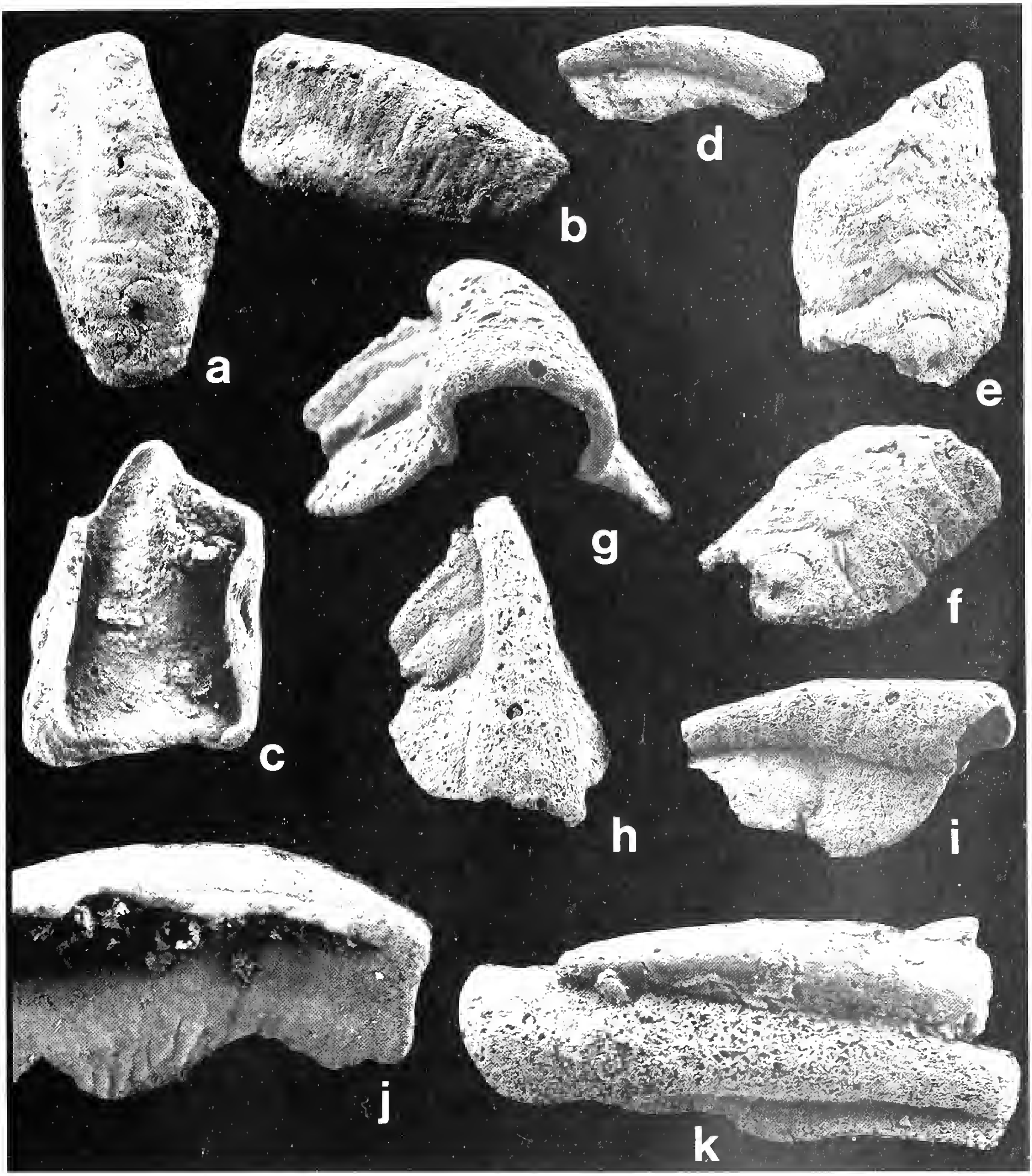
Figs 1–17. *Paracarinachites spinus* (Yu 1984). 1, IGAS-BC-88-30137. 2 and 3, IGAS-BC-88-30138. 4 and 5, IGAS-BC-88-30139. 6, IGAS-BC-88-30140. 7 and 8, IGAS-BC-88-30141. 9 and 10, IGAS-BC-88-30142. 11 and 12, IGAS-BC-88-30143. 13, IGAS-BC-88-30144. 14 and 15, IGAS-BC-88-30145. 16, IGAS-BC-88-30146. 17, IGAS-BC-88-30147. All isolated sclerites, dorsal (Figs 1–5, 7–17), and ventral (Fig. 6) surfaces, from Bed 7, Zhongyicun Member, Yuhucun Formation at Xiaowaitoushan section, Kunyang Phosphorite Mine, Meishucun, Yunnan, China. Magnifications all ×90.



CONWAY MORRIS and CHEN, *Paracarinachites*



TEXT-FIG. 11. Hypothetical reconstructions of partial portions of the scleritome of (*a*) *Zhijinites longistriatus*; (*b*) *Cambroclavus absonus*; (*c*) *Deiradoclavus trigonus*; (*d*) *Deltaclavus graneus*. Text-figure 7*b* is based on Bengtson *et al*. (1990, fig. 70).



TEXT-FIG. 12. *Protopterygotheca leshanensis* Chen in Qian *et al.*, 1979. *a* and *b*, IGAS-BC-88-30192; *a*, dorsal view; *b*, oblique view. *c*, IGAS-BC-88-30193, ventral view. *d*, IGAS-BC-88-30194, lateral view; *e* and *f*, IGAS-BC-88-30195; *e*, dorsal view; *f*, oblique view. *g–i*, IGAS-BC-88-30196; *g*, posterior view; *h*, dorsal view; *i*, lateral view. *j*, IGAS-BC-88-30197, ventral view with internal furrows. *k*, IGAS-BC-88-30198, fused specimen. Isolated sclerites from Bed 37 (*a–c*) and Bed 36 (*d–k*), Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications: *a–d*, ×30; *e*, *f*, *h–k*, ×60; *g*, ×100.

of the flanges may be more or less at right angles to the central axis (Pl. 9, figs 6 and 14; Text-fig. 12*a*) or be inclined posteriorly so that the maximum width is nearer the transverse mid-line (Pl. 9, figs 7 and 11; Text-fig. 12*h*). The flanges, therefore, form wing-like extensions of widely variable shape according to the angles of insertion towards the anterior and posterior ends of the central axis.

Each lateral flange of a sclerite is similar, but minor differences can exist by the asymmetrical development of furrows on one flange (Pl. 9, figs 6, 8, 9, 11, 12; Text-fig. 12*h*). Typically these furrows are transverse, and if they extend to the sclerite margin may disrupt the outline. The furrows grade from fairly open folds to more deeply incised structures. Often the folds are grouped, sometimes radiating outwards. In addition, a few flanges bear longitudinal folds.

In the majority of sclerites the margins are simple, but this may be an artefact of preservation because in some specimens the sclerite edge forms a simple doublure (Text-fig. 12*c*). However preserved, the edge seldom shows internal structure, although rarely incremental units are visible (Pl. 9, figs 4 and 10). The internal surface of the sclerite is normally smooth (Pl. 9, fig. 3), but on occasion a series of transverse furrows that increase in strength towards the margin (Text-fig. 12*j*) have been noted.

With one exception, the sclerites occur isolated. In one individual, however, part of a central axis (and a specimen of *Zhijinites longistriatus*) appears to have fused to another sclerite, the respective axes pointing in opposite directions (Text-fig. 12*k*). It is argued below that the sclerites may have formed an imbricated series, but this particular association seems to be one of post-mortem fusion during phosphatization.

Discussion. In isolation the central axis of these sclerites strongly resembles in overall shape and dimensions specimens of *Paracarinachites sinensis* (Qian and Bengtson 1989). In addition Kerber (1988) noted traces of lateral extensions in his paracarinachitid material from the Montagne Noire, France, but it is difficult to decide whether the absence from the Chinese material is preservational or an original difference that justifies taxonomic separation between it and the French examples (Qian and Bengtson 1989). While the specimens described here from Maidiping can be referred to the paracarinachitids, the precise taxonomic status is somewhat uncertain. Principally, this is because the median row of spines, a diagnostic feature of *Paracarinachites*, is only rarely expressed (Text-fig. 12*e*, *f*). Given the quality of preservation, including the survival of the lateral flanges, it seems implausible that the median spines are lost because of poor preservation. Accordingly, there seems to be reason to retain the genus *Protopterygotheca* at the moment as separate from *Paracarinachites*, and refer to both informally as paracarinachitids.

Attention should be drawn also to problematical fossils from Guizhou that Qian and Yin (1984*a*; see also Wang *et al.*, 1984*b*) referred to as *Solenotia* (type species *S. lata*, also *S. lobata* and *S. elongata*; note *S. incurva* (Wang *et al.* 1984*a*, pl. 21, fig. 17) appears to be a nomen nudum). The material is fragmentary and details are difficult to discern in the published photographs, but some specimens may be comparable to *P. leshanensis* (see in particular Qian and Yin 1984*a*, pl. 5, figs 1 and 4).

DISCUSSION

Scleritome reconstruction

In *Cambroclavus* (Mambetov *in* Mambetov and Repina 1979; Bengtson *et al.* 1990) and *Deltaclavus* gen. nov. fused assemblages suggest that the cataphract scleritome in these taxa was

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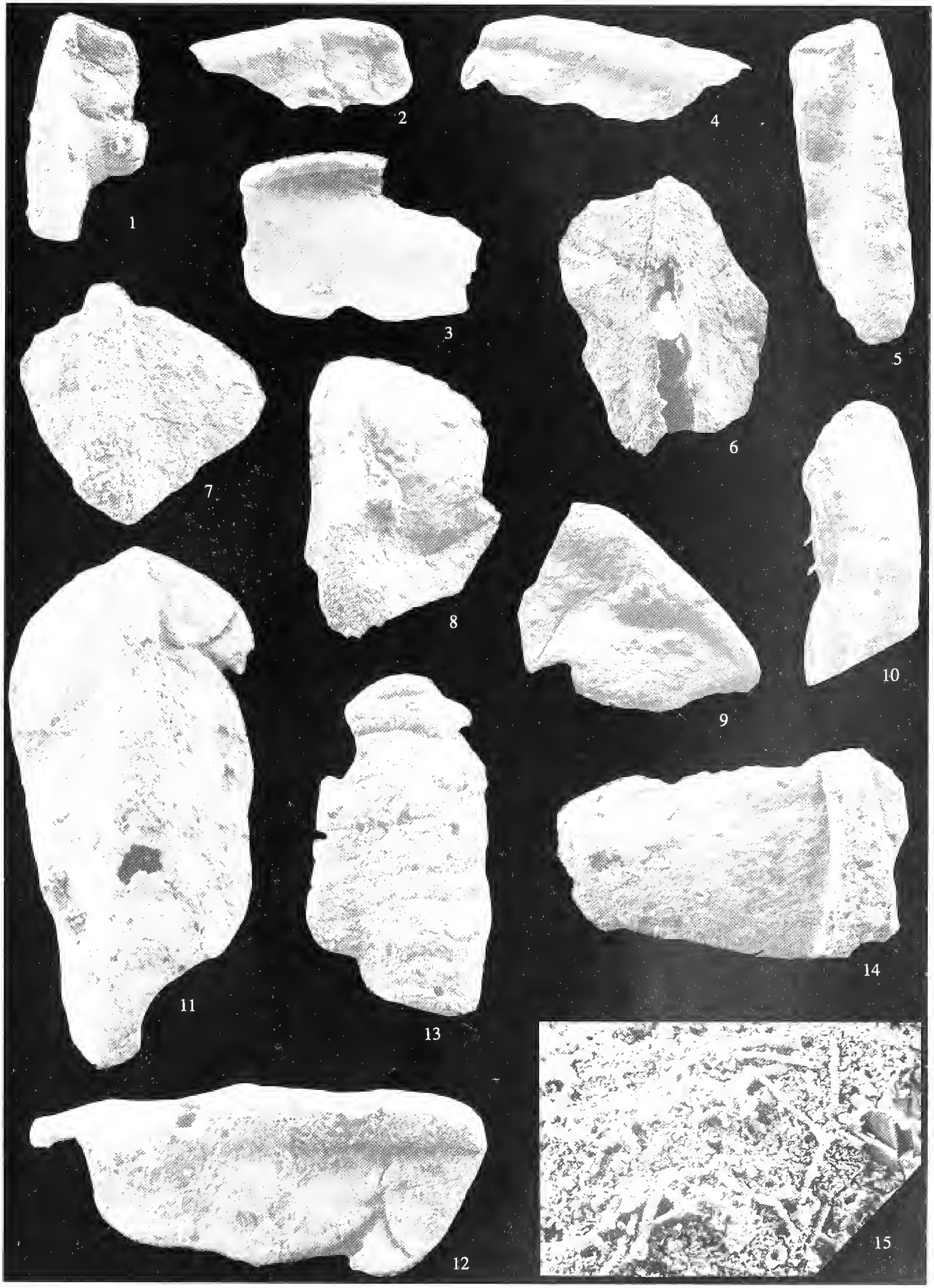
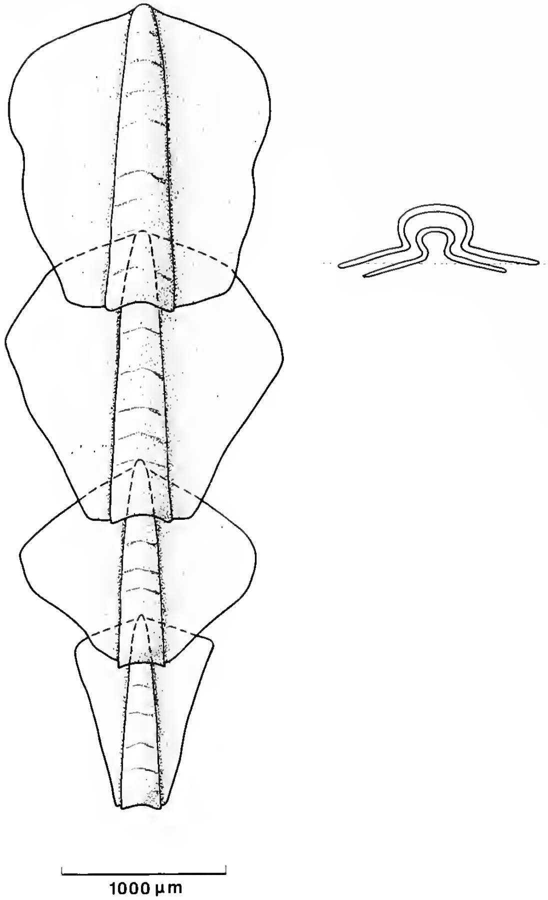
EXPLANATION OF PLATE 9

Figs 1–14. *Protopterygotheca leshanensis* Chen in Qian *et al.* 1979. 1 and 2, IGAS-BC-88-30182; 1, dorsal view; 2, oblique view. 3, IGAS-BC-88-30183, ventral view; 4 and 5, IGAS-BC-88-30184; 4, oblique view; 5, dorsal view; 6, 15, IGAS-BC-88-30185; 6, dorsal view; 15, wall ultrastructure showing diagenetic phosphatization and endolithic borings; 7, IGAS-BC-88-30186, dorsal view. 8 and 9, IGAS-BC-88-30187; 8, dorsal view; 9, oblique view. 10, IGAS-BC-88-30188, dorsal view. 11 and 12, IGAS-BC-88-30189, holotype; 11, dorsal view; 12, lateral view. 13, IGAS-BC-88-30190, dorsal view. 14, IGAS-BC-88-30191, dorsal view. All isolated sclerites from Bed 37, Maidiping Member, Hongchunping Formation at Maidiping section, Emei, Sichuan, China. Magnifications: ×30 (Figs 1–6, 8–12); ×60 (Figs 7, 13, 14); ×400 (Fig. 15).



CONWAY MORRIS and CHEN, *Protopterygotheca*



TEXT-FIG. 13. Hypothetical reconstruction of a partial portion of the scleritome of *Protopterygotheca leshanensis*.

closely integrated with longitudinal files articulating via facets and transverse files interlocking by virtue of congruent shapes (Text-fig. 11*b*, *d*). A reconstruction of the sclerites providing a coating to a worm-like animal thus seems reasonable, in a manner analagous to Recent spicule-bearing animals such as aplacophorans and certain turbellarians (Rieger and Sterrer 1975). In at least some species of *Cambroclavus*, such as a new species from Australia (Bengtson *et al.* 1990), the morphological variation of the sclerites is very wide, and includes many sclerites that depart conspicuously from a bilaterally symmetrical shape. In this new Australian species it was postulated that variability of sclerites occurred within single scleritomes, and that mutual accommodation between differently shaped sclerites could lead to changes in sclerite appearance across the scleritome. Similarly, in *Deiradoclavus* it is supposed that the variability of sclerite shape was typical of individuals, and relatively rapid changes in sclerite shape across the scleritome could be accommodated by a series of minor adjustments.

However, the recognition of articulated series of sclerites in double layers in *Deltaclavus* (Text-fig. 9*d*–*h*) hints at previously unexpected complexities of anatomy in this taxon, although the morphological similarities and comparable age (Text-fig. 2) of *Deltaclavus* and *Deiradoclavus* suggest that their scleritomes did not differ radically from one another. Given the orderly appearance and sense of articulation it seems unlikely that these fused assemblages are taphonomic artefacts, formed for instance by folding together of a single layer. Granted that they are original features, then one interpretation would be to regard them as arm-like extensions, analagous for example to the feeding arms of various pelmatozoan echinoderms. *Deiradoclavus* gen. nov. is known only from isolated sclerites. However, reconstruction as a tightly integrated scleritome (Text-fig. 11*c*) is plausible given the distribution of concave facet-like areas on the dorsal and ventral surfaces.

In contrast to all the above genera, the circular outline of sclerites of *Zhijinites* suggests that they were separate, possibly studding the body surface and isolated by areas of non-mineralized cuticle (Text-fig. 11*a*). What may represent an intermediate case, with some sclerites articulated and others isolated, occurs in *Paracarinachites spinus*. In this taxon some sclerites occur in fused longitudinal rows, whose life association was cogently argued for by Qian and Bengtson (1989). Co-occurring isolated sclerites in part may have been derived by disarticulation of less welded portions of the scleritome, but other sclerites lack any obvious zones of articulation and abutment.

It is questioned whether the remaining species of *Paracarinachites* and *Protopterygotheca* (see above) are either closely related to *P. spinus* or to the zhijinitids (see also Qian and Bengtson 1989, p. 56). One reason to propose this is the distinctive morphology of *P. leshanensis* whose similarity to the type species *P. sinensis* is clear, but whose derivation from any cambroclave morph seems forced. In *P. leshanensis*, where sclerite form is arguably more complete, it is hypothesized that they could have formed an imbricated row (Text-fig. 13). In contrast Qian and Bengtson (1989, p. 56) suggested that 'Several *Paracarinachites* sclerites were positioned close to each other in a cone-like structure, so that the apical ends met in the centre', while similar remarks were also addressed to the possibly related *Scoponodus*.

Biomineralization and mode of secretion

The original composition of the sclerite wall of cambroclaves appears to have been calcareous, with evidence surviving from steinkerns and phosphatic replacement for an originally fibrous ultrastructure. In life the hollow within the sclerites is believed to have been occupied by soft tissue, presumably including secretory epithelia. Such an arrangement is thought more likely than having the sclerites covered with secretory tissue. However, if the calcareous wall was laid down by internal tissue, it seems that initial formation or additions to the scleritome must have entailed patches of secretory tissue that formed a template whose precise expression was governed by the bounding nature of the adjacent sclerites. In this manner accommodation between sclerites to produce a well-integrated scleritome would not need to be under precisely specified genetic control, and would be responsive to local morphology and possibly damage repair.

The relationship between the tissue enclosed in the sclerite and any surrounding tissue is rather problematic. A crude analogy might be drawn with echinoderm ossicles, which contain stereom tissue but are embedded in mesoderm. Although pores are observed on the inner walls of the spinose portion of *Zhijinites* sclerites (Pl. 3, fig. 4) it is not clear if soft tissue extended to the outer margin, especially as the spines are envisaged as projecting free of the body wall.

In *P. spinus* heavy diagenetic phosphatization appears to have obliterated all traces of original mineralogy. However, granted that the fused series described by Qian and Bengtson (1989) represent a primary association, then it is necessary to postulate secretory tissue that lay beneath the sclerite series. In the remaining paracarinachitids the clear distribution of growth lamellae (Kerber 1988; Qian and Bengtson 1989; see also Pl. 9, figs 4 and 10) suggests that secretory tissue formed a mantle-like layer responsible for production of mineralized increments.

Palaeoecology

Scleritome reconstruction of a new species of *Cambroclavus* from Australia (Bengtson *et al.* 1990) was taken to indicate a primarily defensive role, presumably against predators and physical abrasion. The elongate spines arising from the anterior region of each sclerite would be an important contributory factor, but it was also noted that their recurved nature could have assisted in grasping substrates. However, if *Cambroclavus* was a burrowing organism, then one might predict an allometric change in spine size to compensate for increase in body size in comparison with habitation of a substrate of fixed grain size (see Aller 1974 for an analagous example in bivalve molluscs). Tentative evidence from the Australian material, however, did not support such an allometric response.

Systematic position

The relationships of cambroclaves to other major groups remain problematic. Mambetov's (*in* Mambetov and Repina 1979) comparison of the cambroclaves to the protoconodont *Protohertzina* and conodont-like *Rhombocorniculum* seems to be without foundation. Various Chinese workers (e.g. Qian and Yin 1984*b*) have placed the cambroclaves in the Acanthocephala, an endoparasitic group of worms with no known fossil record (Conway Morris and Crompton 1982). This supposition is based on the similarities between cambroclave sclerites, especially of *Zhijinites*, with the proboscis hooks of acanthocephalans (see also Qian and Xiao 1984, p. 79). However, differences in composition, mode of secretion, and recognition in cambroclaves of an integrated scleritome, that at least in *Deltaclavus* includes 'arm-like' structures, all suggest that cambroclaves are unlikely to be related to acanthocephalans. However, in the absence of complete scleritomes and associated soft-part preservation, the wider affinities of this group remain uncertain.

No further light can be thrown either on the wider affinities of the paracarinachitids, other than the tentative proposal that *P. spinus* be regarded as belonging to the cambroclaves, while the remaining species of *Paracarinachites*, possibly together with *Scoponodus* and even *Ernogia* (see above), be regarded as a distinct group. What is clear, however, is that comparisons between paracarinachitids and polyplacophorans (e.g. Yu 1989) are without foundation, a point already cogently made by Qian and Bengtson (1989, pp. 48–49).

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THE OSTRACODERM *PHIALASPIS* FROM THE LOWER DEVONIAN OF THE WELSH BORDERLAND AND SOUTH WALES

by P. R. TARRANT

ABSTRACT. The Lower Devonian ostracoderm *Phialaspis symondsi* differs sufficiently from the type species of the Traquairaspididae, *Traquairaspis campbelli*, to place it within a separate family, the Phialaspididae. This family also includes *Toombsaspis pococki* comb. nov., *T. sabrinae* comb. nov. and *Munchoaspis denisoni* comb. nov. The Traquairaspididae includes *Traquairaspis campbelli* and *Rimasventeraspis angusta* comb. nov. A new reconstruction of the carapace of *Phialaspis symondsi* is given and, from an examination of immature plates, a possible mode of growth is outlined. Likely feeding and respiratory mechanisms are discussed. A new form of jet-aided steering is proposed for phialaspidid ostracoderms.

THE inner surface of a heterostracan ventral median plate was described by Lankester (1868) as *Cyathaspis symondsi*. Later Traquair (1898) described plates with a stellate tubercular ornament as *Psammosteus anglicus*, from which the *Psammosteus* Limestone is named. Wills (1935) and White (1946) described the morphology of the carapace under the name *Phialaspis* combining Lankester's and Traquair's material (transferred to *Traquairaspis* in 1948 by White and Toombs). More recently, Dineley and Loeffler (1976) have added to the knowledge of general traquairaspidid morphology by their descriptions of Canadian material with dorsal shields formed of fused plates.

The bulk of the *Phialaspis symondsi* material described in this work (over 200 specimens) came from Devil's Hole stream section (also known as the Lye Brook: White and Toombs 1948; White 1950*b*; Ball and Dineley 1961) which dissects the Lower Devonian, Downton/Ditton Group transition (White 1950*a*) of the Lower Old Red Sandstone, Morville district, Shropshire. This is mainly the result of sixteen years of collecting by Mr A. M. Tarrant and the author. Also included, are descriptions of specimens collected from the site by the late Mr H. A. Toombs and Professor D. L. Dineley, and material collected to be studied as part of a palaeoecological project when the Nature Conservancy excavated the site in 1981. Material of *Phialaspis symondsi* and *Toombsaspis pococki* collected from elsewhere within the Anglo-Welsh Region (Text-fig. 1) and the Scottish *Traquairaspis campbelli* was also studied.

ANGLO-WELSH LOCALITIES

Details of localities 2–4 and 6–14 are listed in Ball and Dineley (1961). Further information on all the localities given below is deposited with the Nature Conservancy Council, Geological Review Unit, Peterborough, to which enquiries may be directed.

Shropshire (*Clee Hills District*): (1) Barnsland Farm Quarry; (2) Clapgate Quarry; (3) Devil's Hole; (4) Earnstrey Brook; (5) Gardener's Bank; (6) Great Oxenbold Stream; (7) Hudwick Dingle; (8) Kidnall Gutter; (9) Little Oxenbold; (10) New Buildings; (11) New Inn; (12) Oak Dingle; (13) Sudford Dingle; (14) Targrove Quarry. *Phialaspis symondsi* is found at all these localities, with *Toombsaspis pococki* found in addition in a separate horizon at locality 5.

Hereford and Worcester: (15) Birch Hill Quarry, The Trimpley Inlier; (16) Cradley Quarries, The Trimpley Inlier; (17) Common Bach, Dorstone, Black Mountain District; (18) Cusop Dingle, Black

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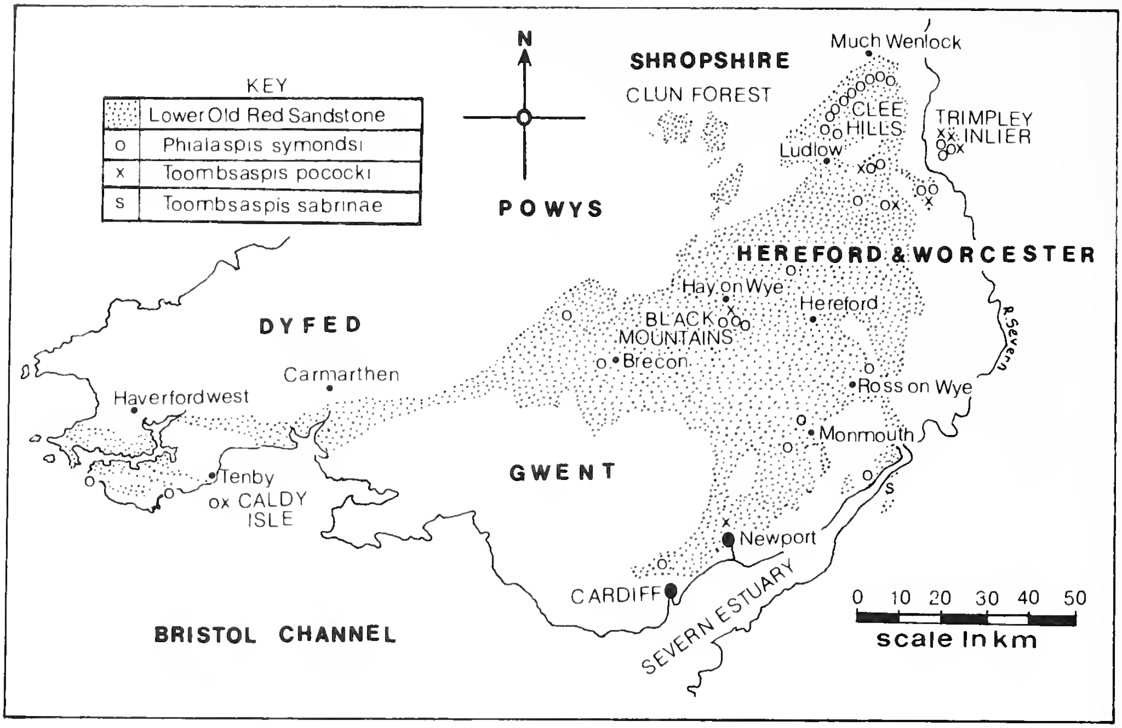


TEXT-FIG. 1. Known phialaspidid localities in the Anglo-Welsh Lower Old Red Sandstone, indicated by symbols as shown in the key.

Mountain District; (19) Eastham Brook, The Trimpley Inlier; (20) Heath Farm, Wolferlow, The Trimpley Inlier; (21) Holbeach House Stream, The Trimpley Inlier; (22) House of the Wood Quarry, Garnon's Hill, Heightington; (23) Hurtlehill Farm Quarry, Heightington; (24) Llan Farm, Dorstone, Black Mountain District; (25) Man Brook, The Trimpley Inlier; (26) Mary Moors, The Trimpley Inlier; (27) Merbach Brook, Ledbury; (28) Park Atwood Stream, The Trimpley Inlier; (29) Ross Motorway, M50 section; (30) Sapey Brook, Thrift Farm; (31) Shatterford, Boundry Brook, The Trimpley Inlier; (32) Westhope Hill, near Hereford; (33) Witchery Hole, Clifton on Teme. *Phialaspis symondsi* found at all localities except 28 and 31, at which *Toombsaspis pococki* was found. Both species present at localities 18 and 33, in the same horizon only at the latter.

Powys: (34) Onen, Court Wood Quarries; (35) Pen-y-lan, Crwcws Wood Quarries. *Phialaspis symondsi* found at both localities.

Gwent: (36) Alteryn Quarry, *Toombsaspis pococki*; (37) Coed-y-coedcae, *Phialaspis symondsi*; (38) Penrhos Farm Quarry, *Phialaspis symondsi*.

Gloucestershire: (39) Lydney, *Phialaspis symondsi*; (40) Sharpness Docks, *Toombsaspis sabrinae*.

Dyfed: (41) Caldy Island, *Phialaspis symondsi*, *Toombsaspis pococki* (several horizons); (42) Freshwater West, *Phialaspis symondsi*; (43) Manorbier Bay, *Phialaspis symondsi*.

MATERIALS AND METHODS

To obtain information about their outer surfaces, the Toombs and Rixon (1950) transfer method was used on several specimens. This entailed mounting the specimens on clear resin, and removing the matrix with acetic acid. Although several specimens prepared reasonably well, the results were mixed. The larger plates had a tendency to be destroyed by the acid owing to the calcite infill of their cancellous spaces. A limited amount of success in tracing the sensory canal system came from impregnating certain specimens with oil of aniseed and viewing them in transmitted light. Often it was necessary to remove the aspidin with dilute hydrochloric acid (White 1935, 1946). Many specimens were not prepared because of the risk of damage to their inner surfaces.

The bulk of material is new and is housed in Ludlow Museum, Shropshire, SHRCM.G – 235 specimens, and in the National Museum of Wales, Cardiff, NMW – 6 specimens. Other specimens studied are from established collections housed in the following museums: British Geological Survey Museum, Kegworth, Notts., BGS (GSM); British Museum (Natural History), London, BMNH; University of Birmingham Geology Museum, BU; National Museum of Canada, Ottawa, NMC; Princeton University Geological Museum, New Jersey, USA, PU; Royal Museum of Scotland, Edinburgh, RSM; W. F. Whittard collection, S.

STRATIGRAPHY AND PALAEOECOLOGY

Most of the heterostracans described in this work came from the Upper Downton Group, Lower Old Red Sandstone, Anglo-Welsh Region. The stratigraphy and sedimentology of this area have been documented by Ball and Dineley (1961); Allen and Tarlo (1963); Allen (1964, 1974*a*, 1974*b*, 1985); and Allen and Williams (1978, 1981). It is dominated by red mudstones, which are interspersed with discrete beds of upwardly fining, current-influenced units of sandstones and intraformational conglomerates. The conglomerates usually hold the largest concentrations of vertebrate fossils.

Most recent workers in the field have considered that they represent infilled freshwater channel complexes, within an extensive deltaic floodplain (Ball and Dineley 1961; Allen and Tarlo 1963; Allen 1964, 1974*a*, 1974*b*).

The area is dissected by the *Psammosteus* Limestone, a pedogenic feature (see Allen 1974*a*, 1985), which divides the Downton from the overlying Ditton. Although rare specimens of *Phialaspis symondsi* have been found above the *Psammosteus* Limestone, this horizon marks a distinctive faunal change, where the phialaspids are replaced by pteraspidiforms (White 1950*a*; Ball and Dineley 1961).

White (1950*a*) used *Phialaspis symondsi* as a zone fossil marking the uppermost Downton, and *Toombsaspis pococki* to mark the underlying zone. The base of the range of *Phialaspis symondsi* is about 30 m below the *Psammosteus* Limestone. Recent field studies (Rowlands and Tarrant, unpublished data), would suggest that the top of its range is considerably less than Ball and Dineley's (1961) claim of *c*. 53 m above the *Psammosteus* Limestone. The bulk of *Toombsaspis pococki* material studied by White (1946), came from 5 m below the *Psammosteus* Limestone at Gardener's Bank, Shropshire, which is the top of its range. Squirrel and Downing (1969) collected fragments which they considered to belong to this species from 158 m below the *Psammosteus* Limestone at Ateryn Quarry, Gwent, which may be the bottom of its range. However, it would appear that the two species substantially overlapped in time.

They have only been recorded together at the Witchery Hole, Clifton on Teme, Hereford and Worcester (Ball and Dineley 1961), where the material was in loose blocks and may have originated from different horizons (M. A. Rowlands, pers. comm.). As Ball and Dineley suggested, this could indicate that they occupied different environments. Following this, the two species are mainly found with different vertebrate faunas. *Phialaspis symondsi* is characteristically found with *Tesseraspis tesselata*, *Anglaspis macculloughi*, *Corvaspis kingi*, *Turinia pagei*, cephalaspids, *Ischnacanthus wickhami* and other acanthodians (Ball and Dineley 1961; Turner 1973). It is also occasionally found with *Protopteraspis gosseleti*, *Pteraspis rostrata* and *Nodonchus* sp. *Toombsaspis pococki* is associated with *Tesseraspsis tesselata*, *Didymaspis grindrodi* and other cephalaspids, the *Goniporus–Katoporus* thelodont fauna, *Ischnacanthus kingi* and other acanthodians (White 1946; Turner 1973).

It would seem that the overlapping vertebrate assemblages of the horizons subjacent to the *Psammosteus* Limestone are related as much to varying ecological conditions as they are to time. Indeed, Karatajute-Timalaa (1978) and Blieck (1984) proposed that the zones of *Traquairaspis symondsi* and *Traquairaspis pococki* should be amalgamated into a single *Traquairaspis* zone. However, because of the reclassification of these species in this work, it is proposed that it should be renamed the *Phialaspis symondsi–Toombsaspis pococki* zone.

As Ball and Dineley (1961) observed, the vertebrate remains are often fragmented, and concentrated in pockets with individual specimens of a similar size, buoyancy, or weight, suggesting that they were probably originally transported, water selected, and in some cases may have been reworked. Their preservation is usually good, often showing fine details, and the vascular cancellous layers are normally not crushed, because of calcite infilling.

SYSTEMATIC PALAEONTOLOGY

Subclass HETEROSTRACI Lankester, 1868

Order TRAQUAIRASPIDIFORME Tarlo, 1962

Diagnosis. (After Dineley and Loeffler 1976). Dorsal shield comprises either single plate or single dorsal disc, rostral and pineal plates, and paired orbital, branchio-cornual or branchial and cornual plates. Orbital, pineal and branchial openings enclosed. Ornamentation of dorsal shield often of elevated, laterally serrated tubercles, commonly with narrow interstitial tubercles or ridges, mainly arranged in cyclomoriform units, sometimes with outer adult plate growth. Ventral disc ovate to elongate, with lateral ornamentation similar to dorsal shield, becomes broader and flatter towards longitudinal midline, or replaced by smooth, flat, ovate central area. Lateral line system variable, ranging from pattern of longitudinal canals and transverse commissures to anastomosing network.

Discussion. Although *Weigeltaspis* may prove to be a traquairaspidiform (Obruchev 1964; Blieck 1983), this has yet to be established. It is possible that the Canadian ?*Traquairaspis* and *Natlaspis* Dineley and Loeffler, 1976, with ornamented ventral central regions, may prove to represent different evolutionary lineages from those species with smooth ventral central regions.

White (1950*a*) realised that the specimens he had described as *Phialaspis pococki* subsp. *cowiensis* White, 1946 were ventral discs of *Traquairaspis campbelli*, and he reclassified *Phialaspis pococki* and *Phialaspis symondsi* as members of the genus *Traquairaspis*. However, following Halstead's (1982) retention of the name *Phialaspis*, the British species can be divided into two distinct morphological groups. They are considered in this work to represent two distinct families, the Traquairaspididae and the Phialaspididae.

Family PHIALASPIDIDAE White, 1946

Type genus. *Phialaspis* Wills, 1935

Other genera assigned. *Toombsaspis* gen. nov., *Munchoaspis* gen. nov.

Diagnosis. Dorsal shield usually comprises seven separate plates. Dorsal disc quadrate, vaulted posteriorly, with median row of large cyclomoriform units on posterior half forming a keel, and usually a dorsal vane. Ventral disc flattening and widening anteriorly with raised, smooth, coffin-shaped central area, situated more posteriorly than anteriorly and enclosed by ornamented margin of disc. Two rows of longitudinally running, large cyclomoriform units on each lateral side of dorsal disc, one row on each lateral side of ventral disc, another row on dorsal side of each branchio-cornual plate. Regions of cyclomoriform adult growth on anterior and lateral edges of dorsal and ventral discs. Paired lateral plates, with, quite frequently, separate paired post oral plates.

Genus PHIALASPIS Wills, 1935

Type species. Cyathaspis (?) *symondsi* Lankester, 1868

Diagnosis. Large advanced Phialaspididae. Dorsal discs more vaulted than ventral disc. Dorsal vane large with two cyclomoriform units, median keel with one. Rostrum enlarged. Branchio-cornual plates with lateral keels terminating posteriorly in lateral vanes. Ventral disc with non-unital cyclomoriform growth between longitudinal units and smooth central region, with three units positioned behind and sometimes fused to its posterior edge. Ornament of stellated tubercles, which are often ringed on the reticular layer by a groove or shelf.

Phialaspis symondsi (Lankester, 1868)

Plates 1–4; Plate 5, figs 2–5; Plate 6; Text-figs 1–10, 13, 14A,B, 15A–G, 16; Table 1

1868 *Cyathaspis* (?) *symondsi* Lankester, p. 27, pl. 6, fig. 5.
1898 *Psammosteus anglicus* Traquair, p. 67, pl. 1, figs 1 and 2.
1935 *Phialaspis symondsi* (Lankester); Wills, pp. 439–444, pls 5–7; text-fig. 4.
1948 *Traquairaspis symondsi* (Lankester); White and Toombs, p. 7.

Holotype. BGS(GSM)31380, ventral disc.

Horizon and localities. Upper Silurian/Lower Devonian. Uppermost Downton and Lowest Ditton Groups, Anglo-Welsh region (see Text-fig. 1).

Referred material. SRCH.G: 213 from Devil's Hole, 13 from Little Oxenbold, 6 from Earnstry Brook, 2 from Barnsland Farm Quarry, 1 from Oak Dingle; NMW: 2 from Cusop Dingle, 1 from Lydney and 3 from Manorbier Bay; material in the BMNH, BGS(GSM), and BU. This material consists of 27 dorsal discs, 14

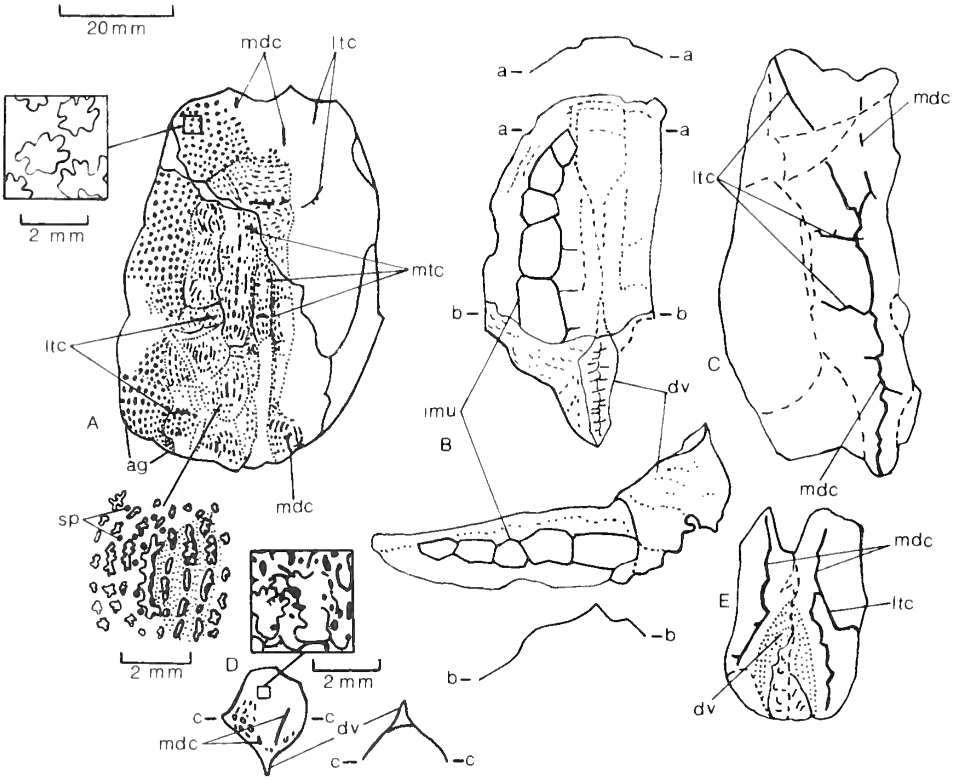
TABLE 1. Maximum dimensions of adult *Phialaspis symondsi* plates in millimetres. Abbreviation: pop, post-oral process.

	Range			Average		
	Length	Width	Ratio of width to length	Length	Width	Ratio of width to length
Dorsal discs	50–70	40–60	0·67–0·96	60	49	0·80
Orbital plates	26–34	12–22	0·44–0·56	30	16	0·52
Pineal plates	9–20	10–20	0·85–1·33	14	15	1·07
Rostrums	13–17	21–24	1·23–1·84	15	22	1·46
Branchio-cornuals	60–80	35–37	0·43–0·55	68	35	0·51
Ventral discs	68–100	42–64	0·54–0·75	81	50	0·61
Lateral plates + pop	26–43	14–24	0·48–0·61	36	20	0·56
Lateral plates − pop	20–31	16–23	0.67–0.90	25	19	0·76
	Curvital dimensions					
Dorsal discs	51–77	50–74	0·76–1·08	64	60	0·93
Branchio-cornuals	94–116			100		
Ventral discs	69–101	44–74	0·61 0.78	83	59	0·71

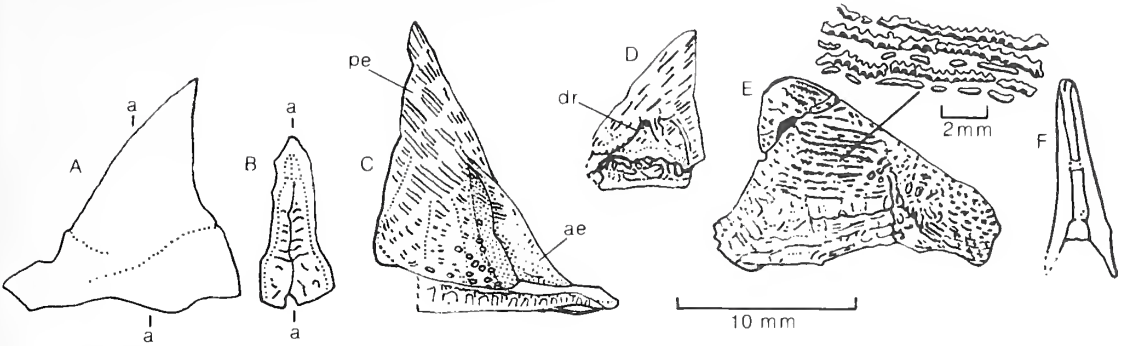
dorsal vanes, 20 orbital plates, 10 pineal plates, 7 rostral plates, 26 branchio-cornual plates, 74 ventral discs, 20 lateral plates, 5 oral plates, plus scales and fragments.

Diagnosis. As for genus.

Description. The dorsal disc (Pl. 1, figs 1 and 2; Pl. 2, fig. 2; Text-fig. 2) is highest and widest about halfway along its length. Its lateral margins are gently scalloped, and the anterior margin is sometimes angled and slightly indented to match the contact with the posterior margin of the pineal plate and the dorso-posterior margins of the orbital plates. The two lateral rows of units are most pronounced at the posterior of the first, most medially-placed row, and along the second row, internal impressions marking their edges can often be seen (Pl. 1, fig. 2; Text-fig. 2B). The cancellae are enlarged under the apex of each unit causing the exoskeleton to swell from 1 to 2 mm in thickness. With the exception of the large tubercle or frequently large tubercles, capping the apex, the tubercles are small and irregular on the units. This contrasts with the larger and more equilateral tubercles found on the peripheral adult zone (Text-fig. 2A), where a longitudinal fold can sometimes be observed on each lateral side of the larger dorsal discs. This is so vestigial that it could hardly be described as a row of units.



TEXT-FIG. 2. *Phialaspis symondsi* (Lankester), dorsal discs. A, part superimposed on counterpart to show ornamentation and incomplete sensory canals, SHRCM.G08137/1–2. B, incomplete and mainly internal mould in plan and lateral views, a–a, b–b, lines of cross section, SHRCM.G08138. C, part superimposed on counterpart to show sensory canal system, SHRCM.G08139/1–2. D, incomplete juvenile showing developing ornament, c–c, line of cross section, SHRCM.G08140. E, incomplete specimen with part superimposed on to counterpart to show sensory canal system, SHRCM.G08141/1–2. Abbreviations: ag, adult growth region; dv, dorsal vane; imu, internal impressions of units; ltc, lateral transverse commissure; mdc, medial dorsal longitudinal canal; mtc, medial transverse commissure; sp, sensory pore.



TEXT-FIG. 3. *Phialaspis symondsi* (Lankester), dorsal vanes, A, lateral view SHRCM.G08142. B, cross section at a–a. C, short high specimen, SHRCM.G08143. D, adolescent specimen, SHRCM.G08144. E, long low specimen, showing ornamental details, SHRCM.G08145. F, ditto, posterior view. Abbreviations; ae, anterior element; dr, developing region; pe, posterior element.

The dorsal vane (Pl. 1, figs 3–5; Text-fig. 3) is triangulate and varies in proportion, ranging from 34 mm long × 21 mm high to 19 mm long × 26 mm high and is 7–10 mm thick at its base. Its two specialized units are often in tandem, with a doubled and thickened cancellous layer which narrows towards the tip and divides at the base to merge with the disc. The rear unit is normally largest. However, the dorsal vane of SHRCM.G08137 (Pl. 1, fig. 6) has an atrophied rear unit, and is mainly formed from the front unit.

Although broken at its anterior end, the dorsal vane SHRCM.G08140 (Pl. 1, fig. 3; Text-fig. 3D) is small, only 17 mm, in height. A depressed region running longitudinally just above its base may indicate an area of growth.

An incomplete and immature dorsal disc SHRCM.G08140 measures 17 mm long × 24 mm double half width (Pl. 2, fig. 2; Text-fig. 2D). Its dorsal vane is shown in section and is 5 mm high × 3 mm thick at the base. The medial longitudinal sensory canals have been exposed and are much closer together than on the larger dorsal discs. All levels of its exoskeleton were present. The surface is pitted with openings on the more complete left lateral and anterior edges. This grades inwards via developing tubercles (Text-fig. 2D) to well-formed large tubercles not arranged in cyclomoriform patterns.

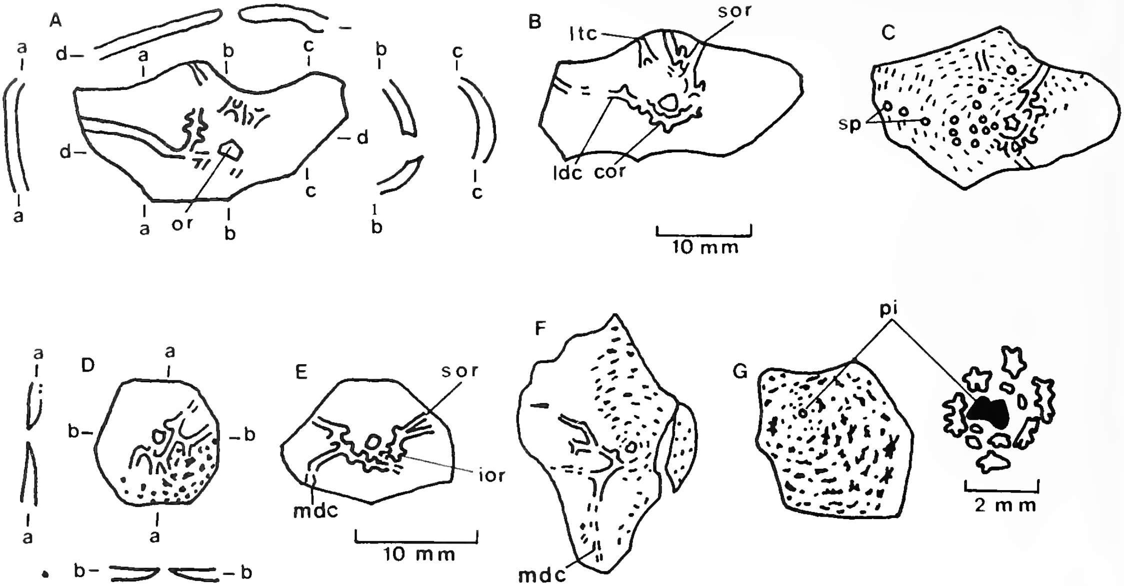
The orbital plates (Pl. 2, fig. 1; Text-fig. 4A–C) are elongate and irregularly diamond-shaped, with usually concave dorsal edges to accommodate the pineal plate. They are curved to present dorsal and lateral sides towards the front, and become flattened towards the back to slope at a dorso-lateral angle. The orbital opening ranges from 2 to 3 mm in diameter; it is on the angle of the dorso-lateral fold, and is usually slightly nearer the anterior edge of the plate than the posterior.

The pineal plate (Pl. 2, fig. 3; Text-fig. 4D–G) is distinguished by its flat and more or less rhomboid shape. There is a centrally placed pineal foramen, which is approximately 1 mm in diameter. The tubercles on the pineal and orbital plates are arranged in concentric rings around the pineal and orbital openings.

The dorsal side of the rostrum (Pl. 2, fig. 6; Text-fig. 5C) is rounded and highest at the posterior edge which is three-pointed, with two concave edges which would have accommodated the front of the orbital plate. The plate tapers towards a tip formed by large horizontally running tubercles.

The ventral pre-oral surface (Pl. 2, fig. 4; Text-fig. 5A) has a raised, flat central region, which probably represents an area of a similar kind to the pre-oral field found on certain pteraspidiforms. With the exception of several long tubercles traversing the anterior half, it is ornamented with small and atrophied tubercles. Posterior to the pre-oral surface and rimmed with a maxillary flange on the angle of ascent, the pre-oral wall ascends vertically to join the posterior undersurface of the plate. The basal laminated layer on the posterior undersurface of SHRCM.G08161 (Text-fig. 5A) is folded and contorted on each side of a shallow median groove.

The larger specimens have proportionally longer pre-oral regions. On the smallest rostrum, NMW88.32G. (Pl. 2, fig. 5; Text-fig. 5D), the pre-oral region is 0·28 times the length and 0·60 times the width of the pre-oral region of SHRCM.G08161. It is broken along its posterior edge, and has all exoskeletal layers present. Its small size and proportions indicate it was from an immature animal. A strong depression on each side of the pre-oral surface shows regions of possible active growth. The basal laminated layer of the posterior undersurface, along its junction with the pre-oral wall, is perforated with vascular foramina often set within large depressions (Text-fig. 5D) which appear to match the contorted conditions found in this region on SHRCM.G08161.



TEXT-FIG. 4. *Phialaspis symondsi* (Lankester). A–C, orbital plates; A, right plate, part superimposed on counterpart to show sensory canal system, a–a, b–b, c–c, d–d, lines of cross section, SHRCM.G08147/1–2; B, right plate showing sensory canal system, NMW88.32G.2; C, right plate, part superimposed on counterpart to show ornamentation and sensory canal system, SHRCM.G08146/1–2. D–G, pineal plates; D, small plate, part superimposed on counterpart to show part of sensory canal system, a–a, b–b, lines of cross section, SHRCM.G08148/1–2; E, small plate, part superimposed on counterpart to show sensory canal system, SHRCM.G08149/1–2; F, fragmentary large plate, part superimposed on counterpart to show part of sensory canal system, SHRCM.G0815/1–2; G, fragmentary large plate showing pineal opening and ornamental details, SHRCM.G08151. Abbreviations: cor, circum-orbital canal; ior, inter-orbital canal; ldc, dorsal longitudinal canal; ltc, lateral transverse commissure; mdc, medial dorsal longitudinal canal; or, orbit; pi, pineal organ; sor, supra-orbital canal; sp, sensory pores.

The branchial opening, located about three-fifths of the way along the length of the branchio-cornual plate (Pl. 3, figs 4 and 5; Text-fig. 6) is dorsally facing and ovate, and ranges in size from 8 × 4 mm to 11 × 7 mm.

The lateral keel embraces the lateral side of the branchial duct and encloses the front of the branchial opening. Its vascular cancellous layer is greatly thickened and individually variable, ranging from 5–12 mm wide × 4–10 mm thick regardless of the size of the rest of the plate. Elongated and longitudinally running rows of tubercles are found on both sides of this region. On its lateral edge, closely spaced, 1 mm thick tubercles overlie smaller primary tubercles (Text-fig. 6B). Occasionally, there are regions of abrasion on the ventral side (Text-fig. 6D).

The lateral vane occupies from the back, one half to one third the length of the branchio-cornual plate and joins the lateral keel. It is solid, triangulate, and dorso-ventrally flattened, with two greatly thickened vascular cancellous layers. Measuring 7 mm thick at its base on SHRCM.G08194, it forms the postero-lateral edge of the branchial opening. The whole vane is tilted postero-laterally, with an elongated region of small and

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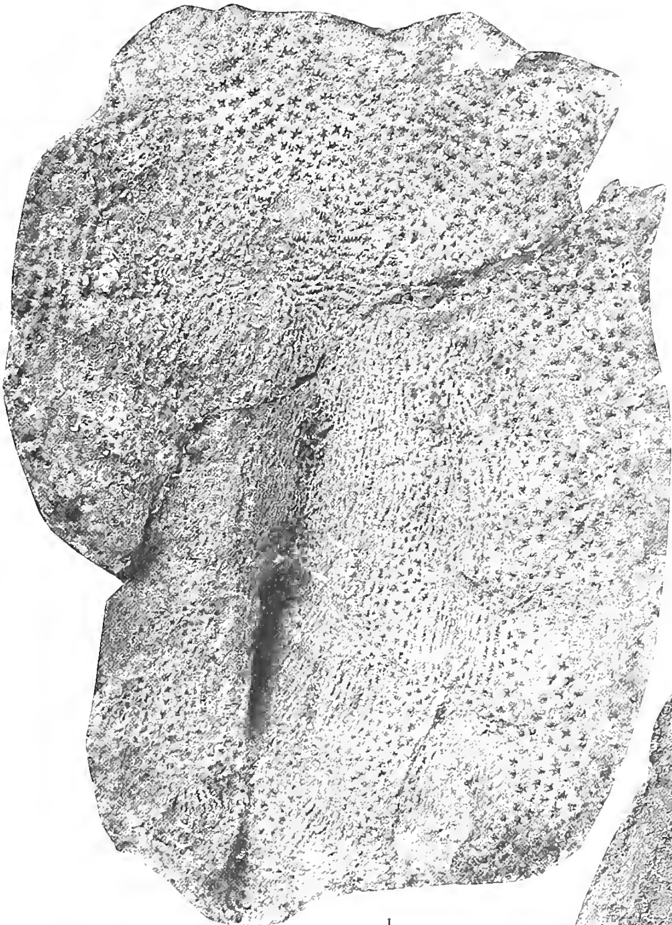
EXPLANATION OF PLATE 1

Figs 1–6. *Phialaspis symondsi* (Lankester), lower Devonian, Welsh Borderland. 1, 2, 6, dorsal discs, × 2; 1, SHRCM.G08166/1, dorsal view of external mould; 2, SHRCM.G08243/1, dorsal view of small internal mould showing impressions; 6, SHRCM.G08166, lateral view of silicon rubber impression showing malformed dorsal vane. 3–5, dorsal vanes, × 2; 3, SHRCM.G08140, external cast of immature vane; 4, SHRCM.G08143, external cast; 5, SHRCM.G08145, external cast.

PLATE 1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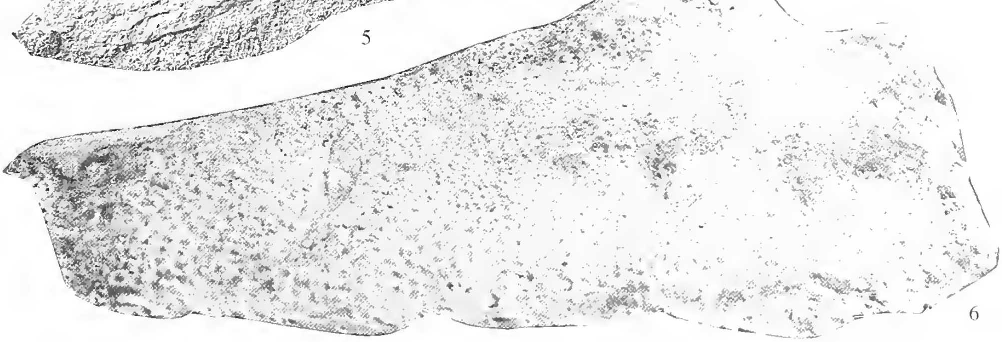
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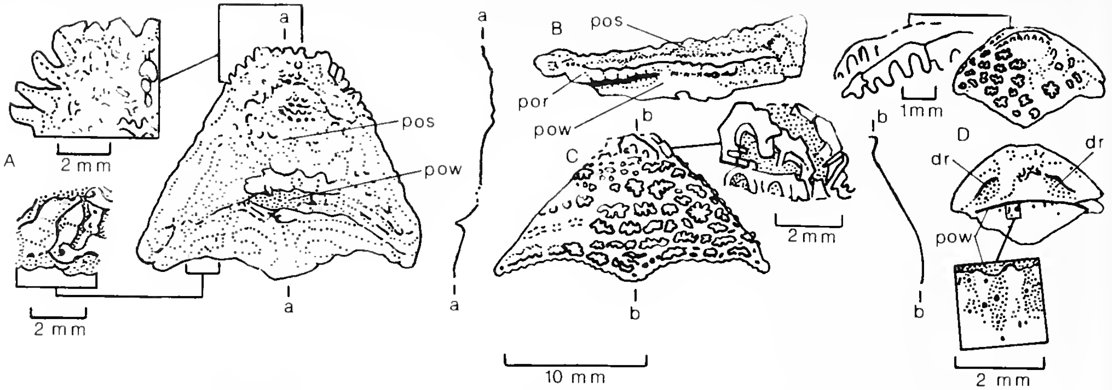

TEXT-FIG. 5. *Phialaspis symondsi* (Lankester), rostral plates. A, ventral view showing details of tip and posterior undersurface, a–a, line of cross section, SHRCM.G08160. B, fragmentary specimen, showing pre-oral wall and part of pre-oral surface, SHRCM.G08161. C, dorsal view showing ornamentation, b–b, line of cross section, SHRCM.G08162. D, immature specimen, part superimposed on to counterpart to show dorsal side with details of ornamentation, and ventral side with details of posterior under surface, NMW88.32G.1*a*/*b*. Abbreviations: dr, developing region; por, pre-oral rim/maxillary brim; pos, pre-oral surface; pow, pre-oral wall.

irregularly shaped tubercles running from the tip to the branchial opening and dividing the dorsal side. On the antero-dorsal side and edge, the tubercles have a tendency to form weak ornamental units and run in rows around the postero-dorsal and ventral sides. Towards the tip, they become elongated and reach up to 1 mm in thickness. The lateral vane is usually terminated at the back by a cyclomoriform unit, which forms a horizontal flange (see Text-fig. 6A) measuring 10 mm long × 5 mm wide on SHRCM.G08153 and SHRCM.G08154. Where the branchial-cornual plate slopes upwards to meet the lateral edge of the dorsal disc, it is composed of a longitudinal row of units (Text-fig. 7B,E). These cover the dorsal side of the branchial duct, encircle the medially facing side of the branchial opening, and are terminated posteriorly by a large unit (Text-fig. 6A,D). They often leave internal impressions marking their edges (Pl. 3, fig. 4; Text-fig. 6B). On the basal laminated layer of SHRCM.G08155 growth ridges run longitudinally between the units and the lateral keel (Text-fig. 6E).

The ornament on the ventral side of the branchio-cornual plate (Text-fig. 6C) curves transversely from the front of the lateral vane, to run parallel with the ventral edge, which is concave to accommodate the lateral edge of the ventral disc. A zone of growth runs parallel with the ventral and dorsal anterior edges, which are angled to match the ventro-posterior edge of the orbital plate and the posterior edge of the lateral plate.

Three elongate and approximately diamond-shaped plates (Pl. 3, figs 1 and 2; Text-fig. 6F,H,I) appear to represent juvenile branchio-cornual plates. Their sizes are: SHRCM.G08157 33 mm long × 13 mm wide; SHRCM.G08156 26 mm long × 10 mm wide; SHRCM.G08158 21 mm long × 8 mm wide. Each is bowed along its length, angled at its front, and tapered towards the back, where a region about 5 mm long projects about 2·5 mm from the lateral side of the plate. This apparently represents the developing lateral vane.

SHRCM.G08156 has been prepared to show typical *P. symondsi* tubercles in various stages of eruption and development (Text-fig. 6F). The inner surface of SHRCM.G08158, shows recently enclosed spaces which form blister-like regions with centrally-placed pores. A 1–2 mm wide margin around the edges is a maze of openings surrounded by enclosing basal laminated growth (Pl. 3, fig. 3; Text-fig. 6I). The longitudinal row of units is

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EXPLANATION OF PLATE 2

Figs 1–6. *Phialaspis symondsi* (Lankester), lower Devonian, Welsh Borderland. 1, SHRCM.G08147/2, right orbital plate, mostly internal view. 2, SHRCM.G08140, immature dorsal disc, in part external mould. 3, SHRCM.G08250, cast of pineal plate. 4, SHRCM.G08160, cast of ventral surface of rostrum. 5, NMW88.32G.1*a*, cast of ventral surface of immature rostrum. 6, SHRCM.G08162/1, cast of dorsal surface of rostrum. All ×4.

PLATE 2


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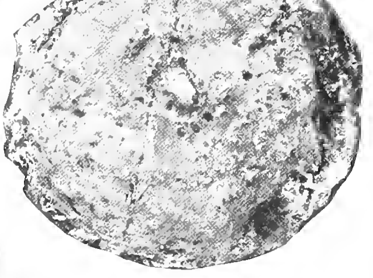
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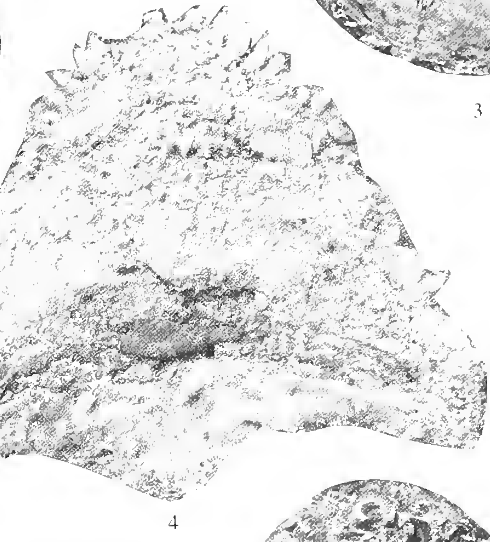
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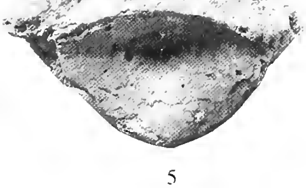
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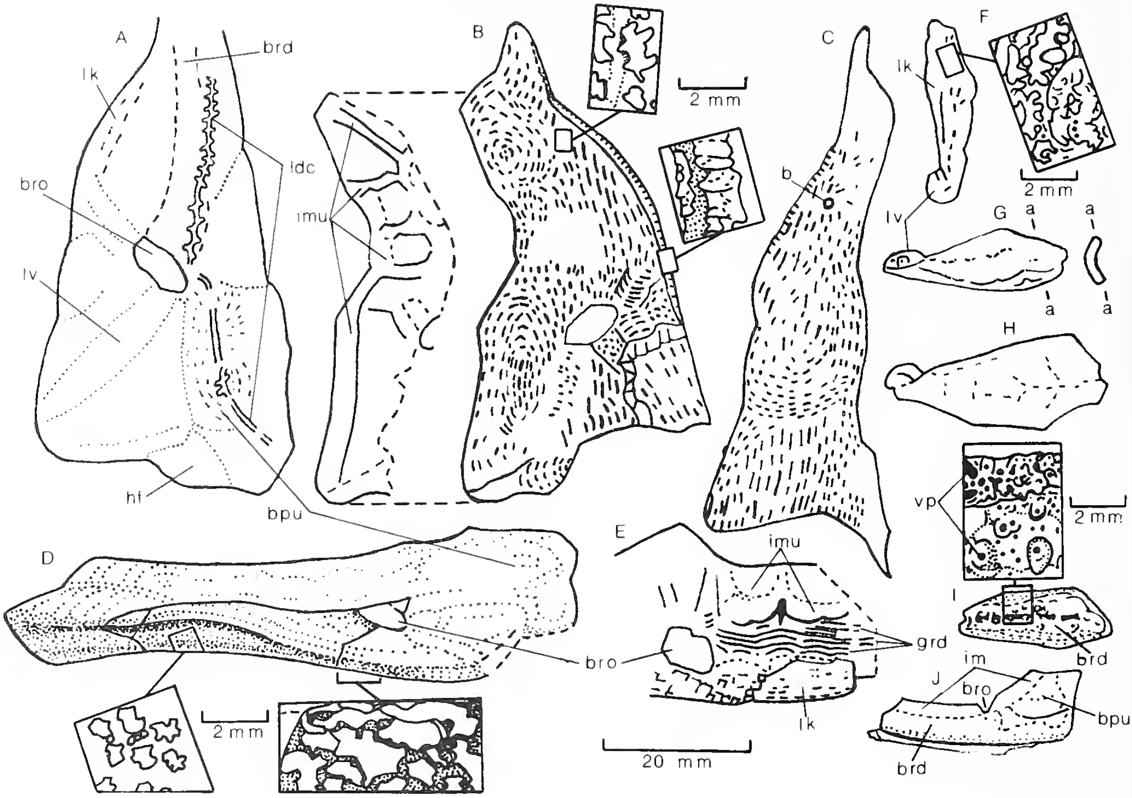
TARRANT, *Phialaspis symondsi*



TEXT-FIG. 6. *Phialaspis symondsi* (Lankester), branchio-cornual plates. A, left plate, dorsal side with part superimposed on counterpart, showing sensory canal system, SHRCM.G08152/1–2. B, right plate, dorsal side showing ornamentation, with dorsal half of counterpart showing inner surface, SHRCM.G08153/1–2. C, right plate, ventral side with part superimposed on counterpart, SHRCM.G08154/1–2. D, left plate, lateral view showing details of worn ornament, BMNH31146. E, fragmentary right plate, lateral view of inner surface, SHRCM.G08155. F,G, juvenile right plate; F, ventral view with detail of ornamentation; G, lateral view; a–a, line of cross section, SHRCM.G08156. H, juvenile right plate, lateral view, SHRCM.G08157. I, juvenile left plate, showing inner surface, SHRCM.G08158/1–2. J, 'adolescent' left plate, lateral view, mainly internal, SHRCM.G08159. Abbreviations: b′, bite; bpu, large posterior unit; brd, branchial duct; bro, branchial opening; grd, growth ridges; hf, horizontal flange; im, inset margin; imu, internal impressions of units; ldc, lateral dorsal longitudinal canals; lk, lateral keel; lv, lateral vane; vp, vascular pores.

missing from these plates, and they are much flatter than the adult branchio-cornual plates. Nevertheless, their branchial ducts run their entire length, which shows that the branchial openings were posteriorly placed and not enclosed. Although the superficial layer was destroyed during preparation, the lateral side of SHRCM.G08157 is 4 mm in thickness, corresponding to the enlargement of the lateral keel.

SHRCM.G08159 (Text-fig. 6J) is an internal mould of an early stage of development of a branchio-cornual

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EXPLANATION OF PLATE 3

Figs 1–5. *Phialaspis symondsi* (Lankester), lower Devonian, Welsh Borderland, branchio-cornual plates. 1, SHRCM.G08158/1, cast of inner surface of immature left plate, ×4. 2, SHRCM.G08156, cast of ventral surface of immature right plate, ×4. 3, detail of 1, ×10. 4, SHRCM.G08153/1, dorsal view of right plate, in part internal mould, ×2. 5, SHRCM.G08152/2, dorsal view of external mould of left plate, ×2.

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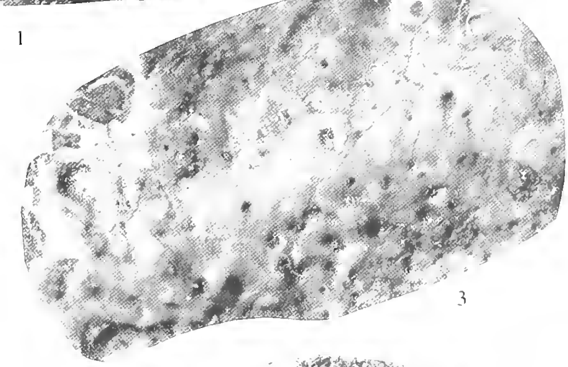

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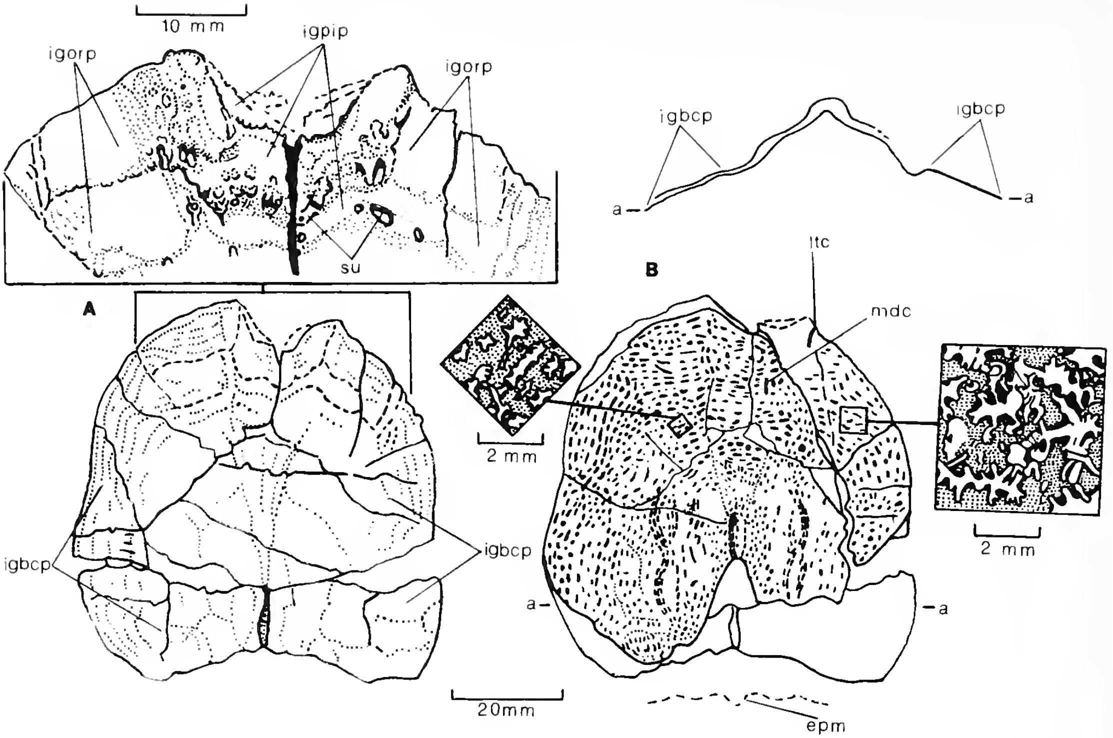
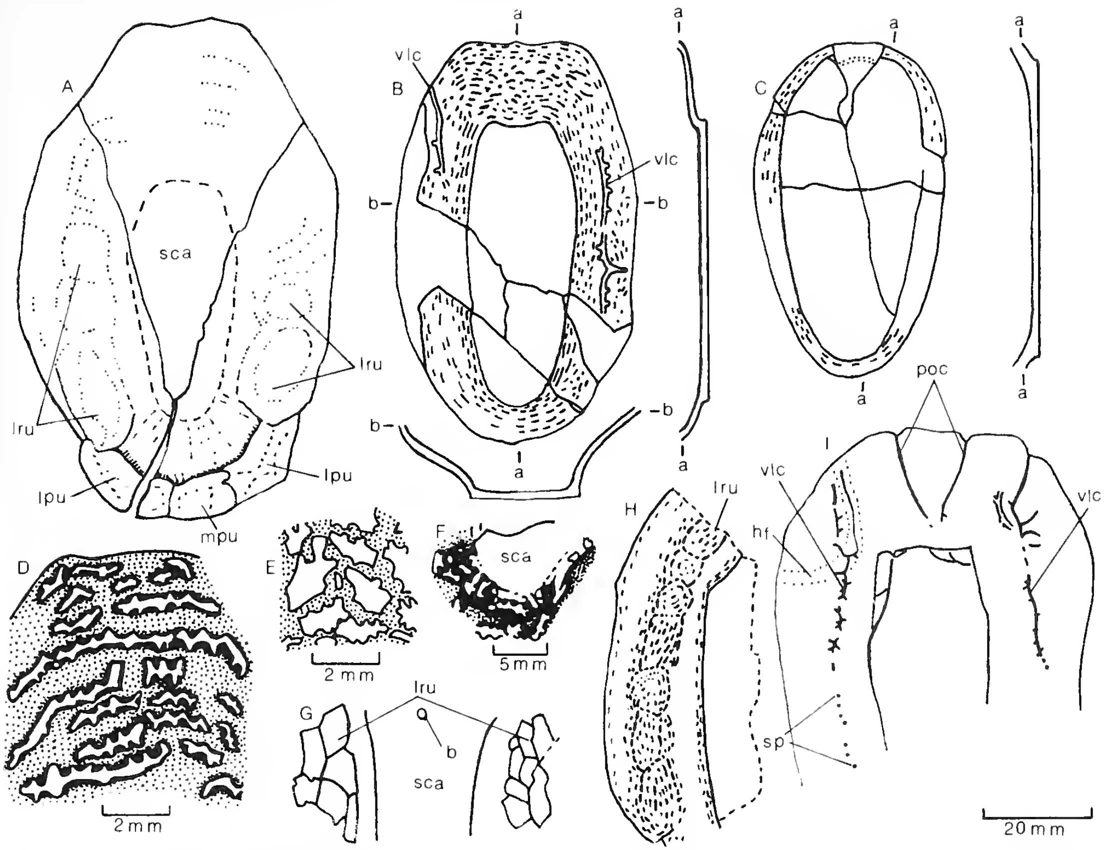


TEXT-FIG. 7. *Phialaspis symondsi* (Lankester), dorsal shield, SHRCM.G08164/1–2. A, internal plan view, with detail of anterior. B, part superimposed on to counterpart to show ornamentation, a–a, line of cross section. Abbreviations: epm, estimated position of posterior margin; igbcp, regions of intergrowth between dorsal disc and branchio-cornual plate; igorp, regions of intergrowth between dorsal disc and orbital plate; igpip, regions of intergrowth between dorsal disc and pineal plate; ltc, lateral transverse commissure; mdc, medial dorsal longitudinal canal; su, sutures.

plate. Although the whole plate only measures 30 mm long, its branchial duct is strongly dorso-ventrally folded as in adult specimens. A cross-section at the front shows all levels of the exoskeleton to be present. The large dorsal posterior unit is present, and is estimated to be two-thirds the size of the equivalent area on the adult plates. A depressed margin, 1–2 mm wide, around its dorsal and posterior edges, and running along the dorsal side of the branchial duct, appears to show regions of active outward growth. An open-ended notch 2 mm wide dissects the margin at the anterior of the posterior unit and appears to represent the start of the enclosure of the branchial opening.

An incomplete dorsal headshield, SHRCM.G08164 (Pl. 4, figs 1 and 2; Text-fig. 7), which is somewhat distorted by compression, consists of the dorsal disc, the inner halves of the branchio-cornual plates, the back of the pineal plate and the dorso-posterior part of the orbital plates, with the omission of the pineal, orbital, and branchial openings. In contrast to the tubercles found in the regions of adult growth of isolated dorsal discs, the tubercles in the regions of adult growth of SHRCM.G08164 vary considerably in size and shape (Text-fig. 7B). Prior to the formation of peripheral adult growth, the dorsal disc acquired the longitudinal units of the branchio-cornual plates, then fused with the back of the pineal plate and the dorso-posterior part of the orbital plates, where sutures can be observed on the inner surface (Text-fig. 7A). As there is no evidence of adult growth on the dorsal edges of the branchio-cornual plates of *P. symondsi*, it appears that during adulthood, the dorsal disc SHRCM.G08164 encroached and intergrew with the longitudinal units of the branchio-cornual plates. Due to a large range in size, it would appear that the pineal and orbital plates of *P. symondsi* were capable of adult growth, and probably on SHRCM.G08164, they contributed to the intergrowth and kept the encroachment of the dorsal disc in check.

In the ventral discs (Text-fig. 8), the flat central area stands proud by 1–2 mm and its surface consists of a



TEXT-FIG. 8. *Phialaspis symondsi* (Lankester), ventral disc. A, internal view, showing attached posterior units, SHRCM.G08165. B, external view showing sensory canal system, a–a, b–b, lines of cross section, SHRCM.G08166/1–2. C, immature plate, a–a, line of cross section, SHRCM.G08167/1–2. D, detail of ornament on left anterior corner, SHRCM.G08168. E, detail of worn ornament on the anterior, BMNH46712. F, abraded posterior, SHRCM.G08169; G, transverse view across midline, showing part of abnormal longitudinal rows of units, SHRCM.G08170. H, part of left side showing longitudinal rows of units, SHRCM.G08171/ I, specimen developed to show sensory canal system, SHRCM.G08171. Abbreviations: b′, bite; hf, healed fracture; lpu, lateral posterior unit; lru, longitudinal row of units; mpu, medial posterior unit; poc, post-oral sensory canal; sca, smooth central area; sp, sensory pores; vlc, ventral longitudinal sensory canal.

smooth sheet of dentine. Regardless of the size of the rest of the disc, it varies considerably in size and proportions, ranging in length from 31 to 60 mm, and in width from 11 mm to an estimated and exceptional 40 mm in BU759. The posterior edge in SHRCM.G08169 is worn, and the adjacent tubercles are abraded and merge with the smooth dentine (Text-fig. 8F).

The tubercles of the ventral disc, in contrast to those of the dorsal disc, are usually of a similar size and normally moderately elongated. Tarlo (1962) recognised that bands of ornamented growth joined each lateral side of the smooth central region to a row of longitudinally running units. These units are cyclomoriform and raised centrally. Although internal impressions marking their edges are sometimes observed, they often protrude internally. There are usually five or more a side, and in SHRCM.G08170 there are two rows crowded together on each side (Text-fig. 8G). A single unit can range in size from 4–15 mm long × 4–10 mm wide.

In certain specimens of ventral discs, the ornament at the front runs horizontally, matching underlying growth ridges. In other cases, it runs at right angles to the growth ridges, before curving round the anterior edges of the longitudinal rows of units, where on SHRCM.G08168 the tubercles join together to become elongated (Text-fig. 8D). This region on BMNH46712 has broadened and abraded tubercles (Text-fig. 8E). The flow of ornament running from the posterior of the smooth central region is also variable, but does not overlie any growth ridges.

Three units forming the posterior end of the ventral disc and uniting the two longitudinal rows of units are only observed clearly as internal impressions on SHRCM.G08165 (Pl. 4, fig. 4; Text-fig. 8A), and probably contacted the antero-ventral ridge scale and the two antero-ventral scales. The medial posterior unit measures 7 mm long × 9 mm wide and the two lateral posterior units both measure 11 mm long × 17 mm wide. As they flatten out at an angle from the vaulted posterior end of the disc, it is likely that they would have been lost after death, and were seemingly often independent of the disc in the younger animals.

Four specimens of immature ventral discs are represented by smooth areas with narrow ornamented margins and no attached units. Each central area is of adult proportions, but as observed on SHRCM.G08167 (Pl. 4, fig. 3; Text-fig. 8C), it rests only slightly proud of the rest of the disc. The anterior and posterior ends of the discs are observed to be flattened internally by a thickening of the cancellous layer.

A specimen (BU77) described by Wills (1935) as cf. *Ctenaspis*, is actually a fragmentary ventral disc from *P. symondsi*. With the exception of a small region of smooth dentine measuring 1 × 2 mm, the superficial layer is missing, leaving the cancellae exposed.

As White (1946) found on *T. pococki*, *P. symondsi* had two lateral plates. The lateral plate is approximately triangular in shape (Pl. 5, figs 2 and 5; Text-fig. 9A–D). It is widest at its anterior end, and tapers towards its posterior edge where it met the branchio-cornual plate. The plate is folded, forming anterior, lateral, and ventral sides, and it is deepest at their junction. The bulk of the plate is ventral in position, where it is flattest. One edge is concave to embrace half of the anterior edge of the ventral disc. On the opposite edge, the plate is folded longitudinally at an angle of 60–90°, to form the 3–4 mm wide laterally facing side, which is angled to meet the ventral edge of the orbital plate. The anteriorly facing side folds inwards at between 20° and 50° from the main body of the plate. It is cradled by a concave region, which at one end forms a projection that would have met the postero-ventral part of the rostrum, and at the other end forms either a truncated mesial edge, or a post-oral process (Text-fig. 9A,C). The post-oral process is partly square in outline, flattened at its free end, and measures about 5 mm long × 10 mm wide. It is too short to occupy the space between the lateral plates, the front of the ventral disc, and the oral region, and must therefore have been paired.

About one third of the lateral plates collected from Devil's Hole have post-oral processes, but the rest show no sign of this structure and must have possessed separate post-oral plates. Older animals may have fused plates. Although the lateral plate, SHRCM.G08174 (Pl. 5, fig. 5; Text-fig. 9D), has an exoskeleton of adult thickness, it measures 19 mm long × 10 mm wide, and is so small that it must represent an immature plate, yet it possesses a well-formed post-oral process.

The ornament on the lateral plates is cyclomoriform, and the post-oral process was formed from a separate cyclomoriform unit. The tubercles in some specimens (Text-fig. 9A) are enlarged and joined together, and tubercles occasionally run at right angles to the main ornamental direction.

Because of their large size, it seems that two anterior lateral plates and one median oral plate were the full complement of oral plates present in *P. symondsi*.

The posterior end of the median oral plate seems to have been as wide, if not slightly wider than the posterior margin of the oral cavity, and somewhat longer than the length of the oral cavity. Therefore it would appear to have rested inside the mouth, where, laterally and posteriorly, it was overlapped by the anterior lateral plates. It ranges in width from 16 to 11 mm, in length from 14 to 12 mm, and is about 6 mm high. It is scoop-shaped, and is ornamented on its outer side and smooth on its inner side and edges (Pl. 5, fig. 4; Text-fig. 9E,F). The inner side (Text-fig. 9F) has an elongated and gently convex central area, which strengthens and widens towards the back. The inner side behind the edge turns outwards to form a narrow lip, which is matched by a thickening of the exoskeleton. On the outside the tubercles are small and narrow and they generally run longitudinally, although they sometimes curve and run at right angles to the main direction. The ornament is abraded in places, in particular on the right lateral side of SHRCM.G08177, and there is a large callus 5 mm

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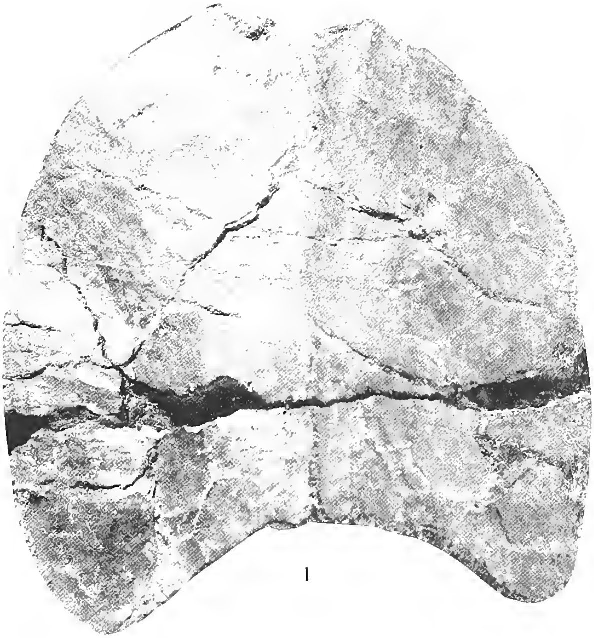
EXPLANATION OF PLATE 4

Figs 1–4. *Phialaspis symondsi* (Lankester), lower Devonian, Welsh Borderland. 1 and 2, SHRCM.G08164/1/2, dorsal headshield, dorsal views of internal mould and silicon rubber impression of external surface, respectively. 3 and 4, ventral discs; 3, SHRCM.G08167/1, external mould of immature disc; 4, SHRCM.G08165, internal view of cast. All × 1.



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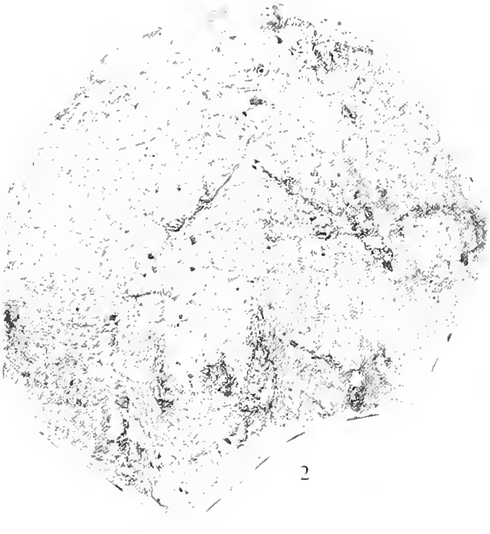

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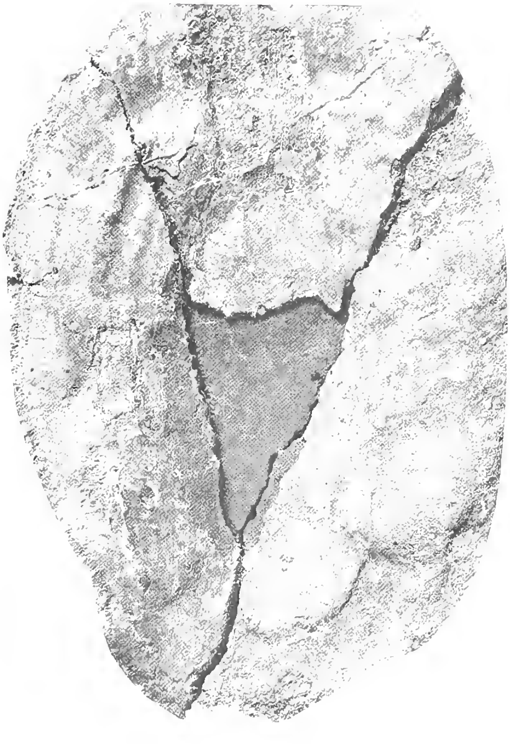

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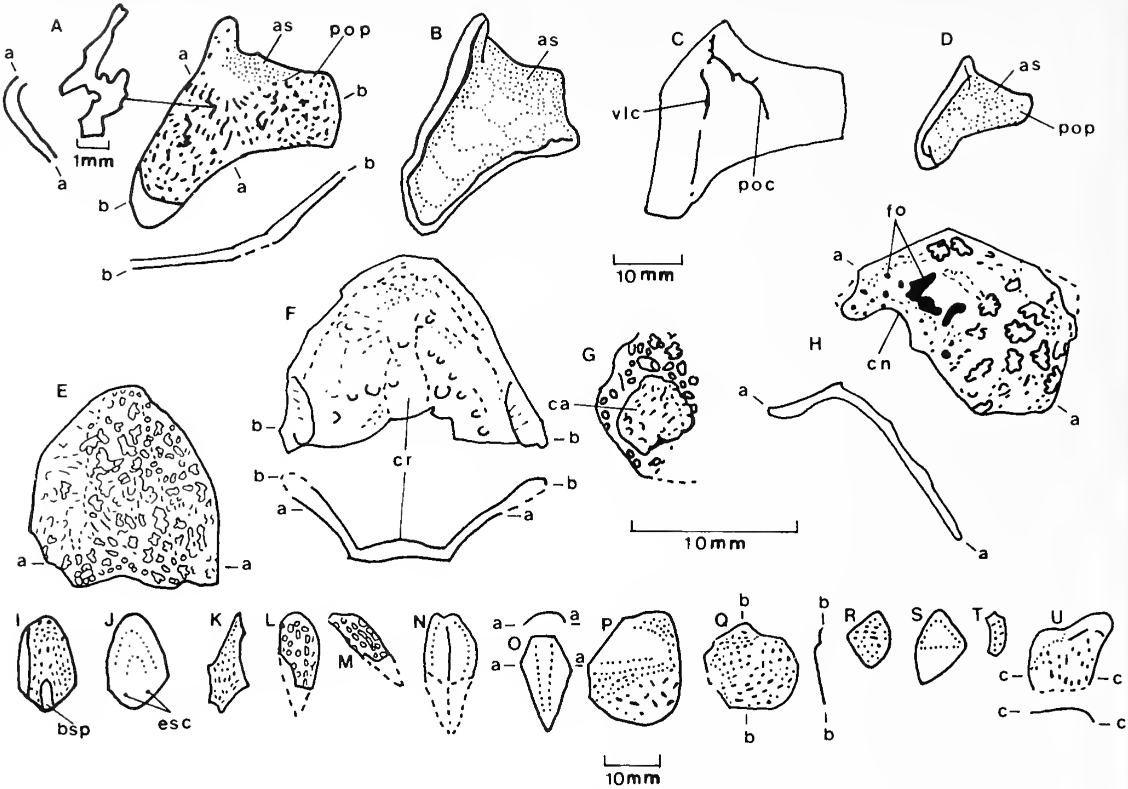
TARRANT, *Phialaspis symondsi*

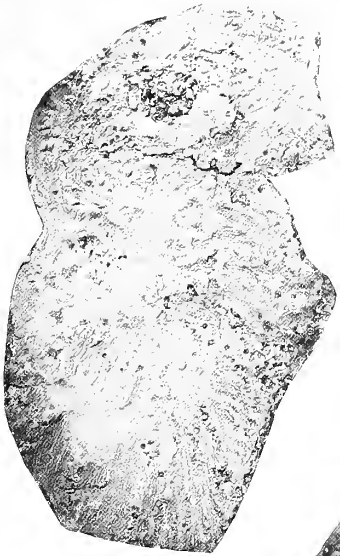


TEXT-FIG. 9. *Phialaspis symondsi* (Lankester), A–D, lateral plates; A, external view of right plate, showing ornamentation, a–a, b–b, lines of cross section, SHRCM.G08173/1–2; B, internal view of left plate, without post-oral process, SHRCM.G08176/1–2; C, right plate developed to show sensory canal system, SHRCM.G08175; D, internal view of immature left plate, SHRCM.G08174. E–H, oral plates; E, internal view of median oral plate; F, ditto, external view, a–a, b–b, lines of cross section, SHRCM.G08177/1–2; G, right posterolateral corner of median oral plate, showing region of abrasion, SHRCM.G08178. H, external view of left anterior lateral plate, c–c, line of cross section, SHRCM.G08179. I–U, scales; I–K, dorsal ridge scale, SHRCM.G08180/1–2; I, external view; J, internal view; K, lateral view; L–M, ventral ridge scale, SHRCM.G08181; L, external view; M, lateral view; N,O, internal views of ventral ridge scales, a–a, line of cross section, SHRCM.G08182, 08183; P,Q, large flank scales, b–b line of cross section, SHRCM.G08190, 08191; R, external view of flank scale, SHRCM.G08185; S, internal view of flank scale, SHRCM.G08184; T, ?caudal scale, SHRCM.G08187; U, incomplete ?ventral lateral scale, c–c, line of cross section, SHRCM.G08189. Abbreviations: as, anterior side; bsp, broken spine; ca, calus; cn, concaved notch; cr, convexed central area; esc, exit pores for sensory canals; fo, foramina; poc, post-oral sensory canal; pop, post-oral process; vlc, ventral longitudinal sensory canal.

EXPLANATION OF PLATE 5

Fig. 1. *Toombsaspis pococki* (White), lower Devonian, Welsh Borderland, BU.2098/1, cast of dorsal headshield, ×4.

Figs 2–5. *Phialaspis symondsi* (Lankester), lower Devonian, Welsh Borderland. 2, SHRCM.G08179, cast of right anterior lateral plate. 3, SHRCM.G08173/1, cast of right lateral plate. 4, SHRCM.G08177/1, cast of median oral plate. 5, SHRCM.G08174, internal view of cast of immature left lateral plate. All ×4.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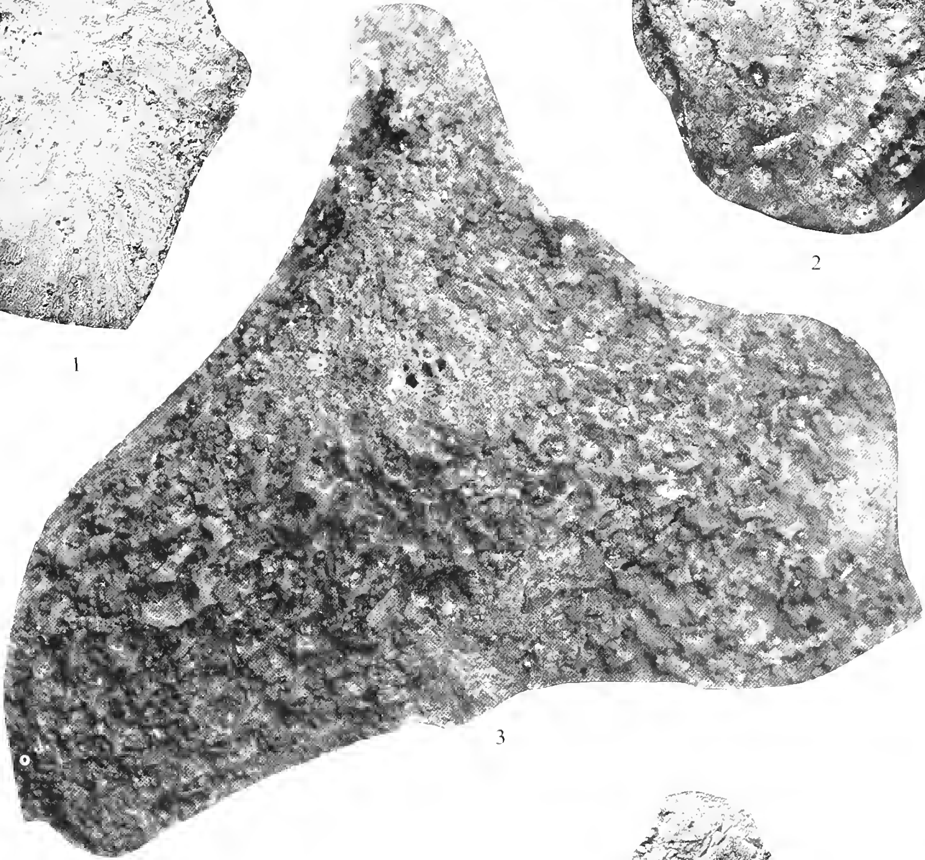
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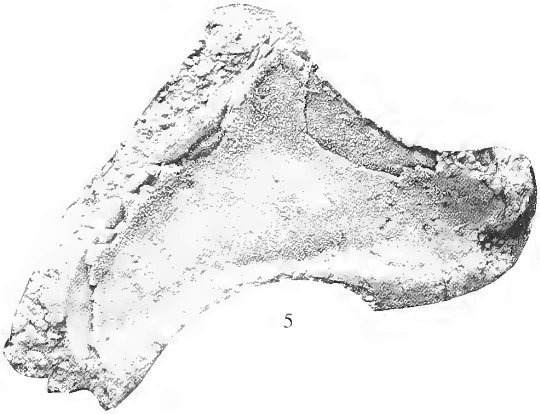
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TARRANT, *Toombsaspis pococki*, *Phialaspis symondsi* long and 2 mm thick, at the posterior end of the right lateral side in SHRCM.G08178 (Text-fig. 9G). The worst of these abrasions appear to have been caused by friction against the anterior lateral plates.

The anterior lateral plate is represented by one specimen SHRCM.G08179 (Pl. 5, fig. 2; Text-fig. 9H). Although much larger, this resembles BMNH24788, a specimen that White (1946) described as possibly an anterior lateral plate from *T. pococki*. It measures 14 × 10 mm and is semicircular and bowed in shape. It rises to 4 mm, around a concave notch on one edge, and flattens towards the opposite edge. The inner surface is smooth, and the tubercles on the outer surface are progressively more abraded towards the raised region, where they are missing. The exoskeleton is pierced by foramina, which radiate in three rows around the concave notch. The largest of these foramina are ovate, 1 mm in diameter, and are angled to point towards the flattened part of the plate. These oral plates presumably lay freely edge to edge, with their raised concave notches lying antero-laterally and facing the anterior edges of the lateral plates. This supposition is based on the shape of the oral cavity, as manifested by its surrounding plates, and the shape and dimensions of the anterior lateral plates.

As White (1946) observed with *Phialaspis*, the sensory canal system was variable, irregular, often asymmetrical, and in *P. symondsi* sometimes segmented. It also ranged considerably in depth within the exoskeleton. Grooves underlying sensory canals can be seen with varying clarity on the internal moulds. These are not to be confused with impressions marking the edges of units (Text-figs 2B and 6B). In places, rows of pores can be traced across the external surface of several specimens (Text-figs 2A, 4C, 8I).

White (1946) considered that *T. pococki* had paired, medial and lateral dorsal longitudinal canals joined by medial and lateral transverse commissures, although he suggested that the lateral dorsal longitudinal canals may have been incomplete or sometimes absent. It is possible that the lateral transverse commissures were occasionally partly joined at their lateral extremities by a longitudinal canal, but I have found no evidence in *T. pococki* or *P. symondsi* to support the presence of lateral dorsal longitudinal canals in the positions suggested by White. Instead, it would appear that they were isolated, except at their anterior end, from the lateral transverse commissures, and are represented by the branchial canals described in *T. pococki* by White (1946). In *P. symondsi*, these run under the longitudinal rows of units on the branchio-cornual plates (Text-fig. 6A).

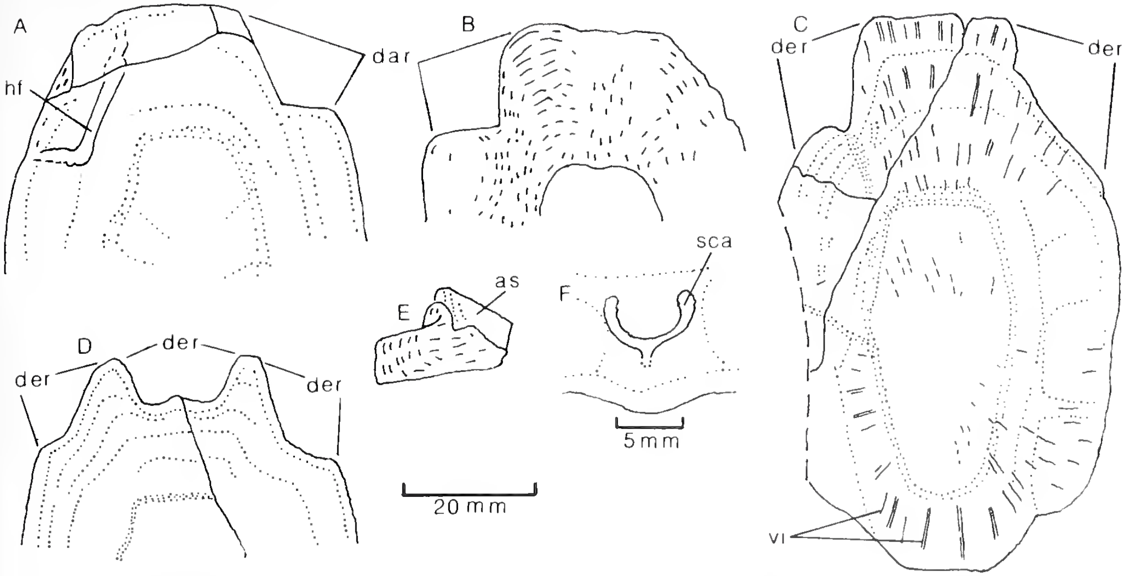
The inter-orbital canal forms a crescent on the pineal plate encircling the posterior and lateral sides of the pineal organ (Text-fig. 4E,F). It joins the medial dorsal longitudinal canals. On each side, it meets a supra-orbital canal and a transverse canal which run on to the orbital plate (Text-figs 4 and 13). and join before meeting the circum-orbital canal (Text-figs 4A–C, 13, 14). The circum-orbital canal completely encircles the orbit. Radiating from it, are the anterior lateral transverse commissure, the lateral dorsal longitudinal canal, and a canal which runs ventrally on to the lateral plate (Text-figs 4C and 9C) and joins the post-oral and ventral longitudinal canals. White (1946) observed no post-oral canals in the *P. symondsi* ventral discs he studied. This is often the case, as the post-oral canals were frequently short and confined to the lateral plates, although sometimes they were present on the ventral discs and V-shaped (Text-fig. 8I). As White noted, the ventral longitudinal canals underlaid the longitudinal rows of units and were varied, often segmented posteriorly (Text-fig. 8B,I).

Because specimens of the rostrum and anterior lateral plates are rare, no attempt has been made to expose possible sensory canals in these regions. However, no evidence has been found for sensory canals either leading to or on them, and it would appear that these were either absent or not linked to the main sensory canal system.

A variety of scales has been found, scattered thinly among the larger *P. symondsi* plates. Most are superficially pteraspid-like, but the anterior flank scales are proportionally much larger.

Dorsal ridge scales measure 8 mm long × 5 mm wide to 17 mm long × 16 mm wide. They are rounded and flattened anteriorly and rise towards the back to create an overlapping region where, although broken on SHRCM.G08177 (Text-fig. 9I–K), they appear to have been crowned with a low spine. The undersurface is gently dished, with two exit pores near the back for the medial dorsal longitudinal sensory canals. The ventral ridge scales range from 8 mm long × 4 mm wide to over 17 mm long × 9 mm wide. They are elongated and spinate (Text-fig. 9L–O), with a small anterior region of attachment angled at about 60° from a hollowed, posterior undersurface. This shows that they were considerably raised and possibly, overlapped strongly.

Several flank scales, including two very large specimens (Text-fig. 9P,Q), are asymmetrical and somewhat flattened, and range in size from 11 × 11 mm to 16 × 18 mm. A depressed region running across one anterior corner indicates an overlapped region. the majority of flank scales collected are smaller, ranging from 7 mm long × 8 mm wide to 10 mm long × 13 mm wide. They are diamond shaped (Text-fig. 9R,S) and folded longitudinally to leave a slightly raised posterior and a somewhat flattened anterior corner, suggesting regions of overlap. Several possibly incomplete, anterior ventral lateral scales are asymmetrical, elongated, and folded longitudinally, to present two unequal sides (Text-fig. 9U). They range from 15 mm long × 10 mm wide to over 15 mm long × 15 mm wide. Two small crescent scales are possibly caudal in origin (Text-fig. 9T).



TEXT-FIG. 10. *Phialaspis symondsi* (Lankester), regions of injury. A–D, on anterior parts of ventral discs; A,B,C, SHRCM.G3802/G08168/G08195.1–2 respectively; D, BGSGSM31380. E, deformed lateral plate, SHRCM.G08196. F, scar on longitudinal unit of ventral disc, SHRCM.G38197. Abbreviations: as, anterior side; dar, damaged region; der, deformed region; hf, healed fracture; sca, scar; vi, vascular impressions.

Injuries and predation scars. White (1946, figs 53 and 54) observed the impression of a healed fracture in the left anterior corner of the *P. symondsi* ventral disc BMNH194. The injury had healed perfectly showing, as White suggested, that the injury must have happened some time before the animal's death. Of ventral discs collected from Devil's Hole which were complete enough to observe the anterior portion, 44% showed injuries like the fracture described by White (Pl. 6, fig. 5), which suggests a common specific kind of injury. Although many of these injuries consist of healed fractures, on several specimens one or both antero-lateral corners are missing (see Pl. 6, figs 3–5; Text-fig. 10A–D). This shows a failure of the broken components to knit. In certain individuals (Text-fig. 10B), narrow regions of outward growth, running across these more severe injuries, show that the animals died soon after their occurrence. In contrast, other specimens (Text-fig. 10C,D) show a reasonable amount of post-injury plate growth. These injuries are extreme in the type specimen BGS(GSM)31380 (Text-fig. 10D), where both antero-lateral corners and a medially placed segment at the front are missing. A deformed, right lateral plate (Text-fig. 10E) has the usual concave contact edge with the ventral disc straight. This may correspond to the injuries on the ventral discs.

A ventral disc SHRCM.G08170 and a branchio-cornual plate SHRCM.G08154 (Text-figs 6G and 8C) are both pierced by a 1·5 mm wide circular hole. Tarlo (1966) observed a hole of a similar kind in the branchial plate of *Psammosteus praecursor*, which he considered was caused by a crossopterygian bite. It is possible that the holes in *P. symondsi* may have been caused by the bite of a large ischnacanthid. Much the same may apply to a well-healed, semi-circular scar on a longitudinal unit of the ventral disc SHRCM.G38197 (Text-fig. 10F).

Remarks. Dineley (1964) described a dorsal disc, NMC10373, from the Knoydart Formation, Nova Scotia, Canada, which he considered was sufficiently close to the specimens from the Anglo-Welsh region to call it *Traquairaspis symondsi*. However, until more Nova Scotian material is described, it is unjustifiable to consider that this specimen belongs to *P. symondsi*, and it is probably best referred to as *Phialaspis* sp.

Genus TOOMBSASPIS gen. nov.

Etymology. In remembrance of the late Mr H. A. Toombs, and *aspis*, Greek, shield.

Type species. Phialaspis pococki White, 1946

Other species assigned. Toombsaspis sabrinae (White, 1946)

Diagnosis. Small phialaspidids with lateral keels. Low dorsal vane. Ventral, longitudinal cyclomoriform units against each lateral side of ventral, smooth central area. Ornament of stellated, equilateral and elongated tubercles divided by fine ridges. Ventral disc tubercles elongated on sides, in stacked V-shapes at back.

Toombsaspis pococki (White, 1946)

Plate 5, fig. 1; Text-figs 1, 11, 14C–G, 15H; Table 2

1946 *Phialaspis pococki* White, pp. 217–229, pl. 12, fig. 1; figs 1, 3–8, 12–19, 22–27, 31–35, 39, 40–44, 55.

1948 *Traquairaspis pococki* (White); White and Toombs, p. 55, pl. 7, fig. 1.

Holotype. BMNH24511 dorsal disc.

Horizon and localities. Upper Silurian/Lower Devonian, Upper Downton Group. The Lower Old Red Sandstone of the Anglo-Welsh region (Text-fig. 1).

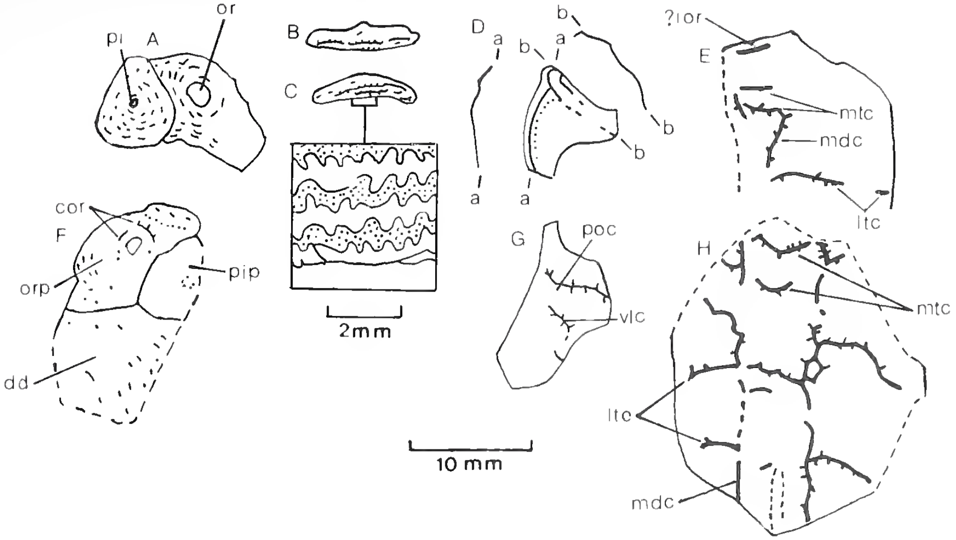
TABLE 2. Maximum dimensions of *Toombsaspis pococki* plates in millimetres. Abbreviation: pop, post-oral process.

	Range			Average		
	Length	Width	Ratio of width to length	Length	Width	Ratio of width to length
Dorsal discs	22–31	22–29	0·73–1·00	28	25	0·89
Orbital plates	11–13	7	0·53–0·63	12	7	0·58
Pineal plates	5–7	6–7	1·00–1·20	6	6	1·00
Rostrums	2	9	4·5			
Branchio-cornuals	25–29	6–7	0·24	27	6·5	0·24
Ventral discs	32–39	18–25	0·53–0·69	35	22	0·63
Lateral plates + pop	8	7	0·87			
Lateral plates − pop	14	7	0·50			
	Curvital dimensions					
Dorsal discs	22–31	24–31	0.89–1.09	28	27	0·96
Ventral discs	33–40	24–30	0·68–0·80	36	28	0·77

Referred material. Specimens housed in the BMNH (especially BMNH24751 and BMNH24568–9) and BU (especially BU2096–2102).

Diagnosis. Dorsal and ventral discs approximately evenly vaulted. Dorsal vane small with one cyclomoriform unit, dorsal median keel with two. Rostrum short. Dorsal disc tubercles long on units, equilateral on periphery.

Description. Internal impressions marking the edges of cyclomoriform units are not usually found, although White (1946) observed internal impressions in the dorsal disc BMNH24512, which he considered were left by sensory canals. These appear to resemble the internal impressions marking the edges of units in the dorsal discs of *P. symondsi*.



TEXT-FIG. 11. *Toombsaspis pococki* (White). A, pineal plate fused to orbital plate, BMNH24568–9. B, dorsal view of rostral plate, BMNH24751. C, ditto, anterior view, with detail of tip ornamentation. D, right lateral plate, a–a, b–b, lines of cross section, BU2097. E, internal view of left anterior side of dorsal disc showing sensory canals, BU2100*a*. F, fragmentary headshield, showing left orbital plate, and part of pineal plate and dorsal disc, BU2098. G, right lateral plate showing sensory canal system, BU481*b*. H, internal view of fragmentary dorsal disc showing sensory canals, BU2101. Abbreviations: cor, circum-orbital sensory canal; dd, dorsal disc; ?ior, possible inter-orbital sensory canal; ltc, lateral transverse sensory commissures; mdc, medial dorsal longitudinal sensory canal; mtc, medial transverse sensory commissures; or, orbital opening; orp, orbital plate; pi, pineal opening; pip, pineal plate; poc, post-oral sensory canal; vlc, ventral longitudinal sensory canal.

The dorsal disc is similar in shape to that of *P. symondsi* and two longitudinal rows of cyclomoriform units are found on each lateral side. The dorsal vane ranges from 2 to 3 mm in height and 6 to 9 mm in length.

The orbital plate (Text-fig. 11 A,F), which is more gently curved than that of *P. symondsi*, is approximately ovate to diamond shaped. The orbital opening ranges from 1 to 1·5 mm, in diameter.

The pineal plate (Text-fig. 11 A) is triangular in shape, with the greatest width at the posterior end. The pineal organ is centrally placed and penetrates the surface of the plate. The ornament on both the pineal and orbital plates is cyclomoriform, encircling the openings. BU2098 (Pl. 5, fig. 1; Text-fig. 11 F) is a fragment of a dorsal headshield showing plate fusion between the dorsal disc, left orbital plate and pineal plate. The pineal organ can only be seen as an internal impression on the counterpart. The orbital plate forms a ridge at its anterior edge, where it would have met the rostrum. BMNH24568–9 (Text-fig. 11 A), identified by White (1946) as an orbital plate, is a pineal plate fused to a right orbital plate.

The rostrum BMNH24751 (Text-fig. 11 B,C) was originally considered to have been a pineal plate (White 1946). It is proportionally much shorter than the immature *P. symondsi* rostrum, and more closely resembles that of ?*Traquairaspis adunata* Dineley and Loeffler, 1976, with elongated tubercles running in rows across its anterior end and no prominent anterior apex.

The branchio-cornual plates (White 1946) are proportionally flatter and less massive than those of *P. symondsi* and, with no lateral vanes, their shape is generally closer to those of *Traquairaspis campbelli*. The branchial opening is about 2·5 mm long × 1·5 mm wide. It faces dorso-laterally and is located at about three-fifths along the length of the plate from the front. The tubercles on the dorsal side tend to be elongate, and a row of cyclomoriform units overlies the lateral dorsal longitudinal sensory canal.

Excluding the smooth central area, the ventral disc (White 1946) is more vaulted than that of *P. symondsi* and, on average it has proportionally larger central area. This ranges from 24–27 mm in length to 10 to 12 mm in width. There is a well-defined row of cyclomoriform units resting against each side of the central area, with no intervening rows of ornamented growth.

Although much smaller, the lateral plates (Text-fig. 11 D,G) closely resemble those of *P. symondsi*. They usually have an attached post-oral process. Nevertheless, White (1946) illustrated a specimen, BU4816, with the post-oral process apparently missing (Text-fig. 11G). White also described a possible anterior lateral plate BMNH24788 and a ridge scale BMNH24759. These appear to be similar to their corresponding parts in *P. symondsi*.

The sensory canal system (Text-figs 11E,F,H and 14) is incompletely known, but appears to be arranged similarly to that of *P. symondsi*. However, the dorsal lateral transverse commissures are longer, and the inter-orbital canal may have extended into the anterior edge of the dorsal disc (Text-fig. 11E).

Remarks. *T. pococki*, which retains more in common with the earlier Traquairaspididae than *P. symondsi*, must be considered as a more primitive phialaspidid. The specimens of a traquairaspidiform from the Red Bay Series, Fraenkelryggen Formation, Spitsbergen, considered by Blieck (1983) as *Traquairaspis* cf. *pococki*, are considerably larger than comparable Anglo-Welsh *T. pococki* specimens, and are provisionally assigned to Traquairaspidiform fam., gen. et sp. indet.

Toombsaspis sabrinae (White, 1946)

1946 *Phialaspis pococki* var. *sabrinae* White, pp. 217–229, pl. 12, figs 2–4; figs 2, 9–11, 20, 21, 28–30, 56.

Holotype. S4, dorsal disc (White 1946).

Type horizon and locality. Upper Silurian/Lower Devonian, Upper Downton Group, Lower Old Red Sandstone, Sharpness, Gloucestershire, England (Text-fig. 1).

Diagnosis. Dorsal disc approximately 30 mm long with equilateral tubercles. Dorsal vane large with long median tubercle, continuous with dorsal keel.

Genus MUNCHOASPIS nov.

Etymology. After Lake Muncho, British Columbia, and *aspis*, Greek, shield.

Type species. *Traquairaspis denisoni* Dineley, 1964.

Diagnosis. Dorsal disc approximately ovate, attaining length of 100 mm, with median keel, no dorsal vane, longitudinal carina on each lateral side marking the change in vaulting and double cyclomoriform whorl on the anterior. Ornament in long fine ridges which run parallel to the anterior and lateral edges.

Munchoaspis denisoni (Dineley, 1964) comb. nov.

1964 *Traquairaspis denisoni* Dineley, pp. 211–215, pl. 38; text-figs 1–4.

Holotype. NMC10371, dorsal disc.

Type horizon and locality. Silurian, Ludlow/Pridoli, North West of Lake Muncho, British Columbia, Canada.

Diagnosis. As for genus, the only known species.

Remarks. Dineley (1964) described several incomplete ventral discs from Canada, which he considered were indistinguishable in outline from the British ones. The smooth ventral central region, surrounded by a gently sloping ornamented brim with peripheral adult growth impressions, is a further typical phialaspidid characteristic. The early occurrence of this species would appear to strengthen Dineley and Loeffler's (1976) claim for a traquairaspidiform evolutionary centre in Western and Arctic Canada.

Family TRAQUAIRASPIDIDAE Kiaer, 1932

Type genus. Traquairaspis Kiaer, 1932

Other genus assigned. Rimasventeraspis nom. nov.

Diagnosis. Ventral disc with narrow ornamented margins, steep lateral sides each with a longitudinal row of elongated tubercles surrounded by cyclomorial fine ridges. The posterior edge sometimes medially notched. Large ventral central area extending to posterior edge, either totally smooth, partly subdivided, or with irregular dentine ridges, and on the anterior half, ventral medial commissures and post-oral sensory canals.

Genus TRAQUAIRASPIS Kiaer, 1932

Type species. Cyathaspis campbelli Traquair, 1913

Diagnosis. Dorsal disc not fused to adjacent plates, ornamented with twelve or more, alternating, longitudinally running rows of small cyclomoriform units. Low dorsal, postero-medial keel. The branchio-cornual plates narrowly keeled behind the enclosed branchial openings. Two distinct types of ventral discs; type 1- smooth central area extending the length of plate (White 1946), type 2-posterior margin deeply notched, median region with a maze of dentine ridged units (Tarlo 1960).

Traquairaspis campbelli (Traquair, 1913)

Text-fig. 12; Table 3

1911 *Cyathaspis* n.sp. Traquair in Campbell, p. 66.
1913 *Cyathaspis campbelli* Traquair in Campbell, p. 932.
1932 *Traquairaspis campbelli* (Traquair); Kiaer, pp. 25–26, pl. 11.
1946 *Phialaspis pococki* subsp. *cowiensis* White, p. 239, figs 36–38.

TABLE 3. Maximum dimensions of *Traquairaspis campbelli* plates in millimetres.

	Average		
	Length	Width	Ratio of width to length
Dorsal disc	39	27	0·69
Branchio-cornual	39	11	0·28
Ventral disc type 1	44	27	0·61
Ventral disc type 2	49	22	0·44

Holotype. RSM1960. 14. 1.

Horizon and locality. Upper Silurian, Pridoli, Stonehaven, Kincardineshire, Scotland.

Referred material. Specimens in the BMNH.

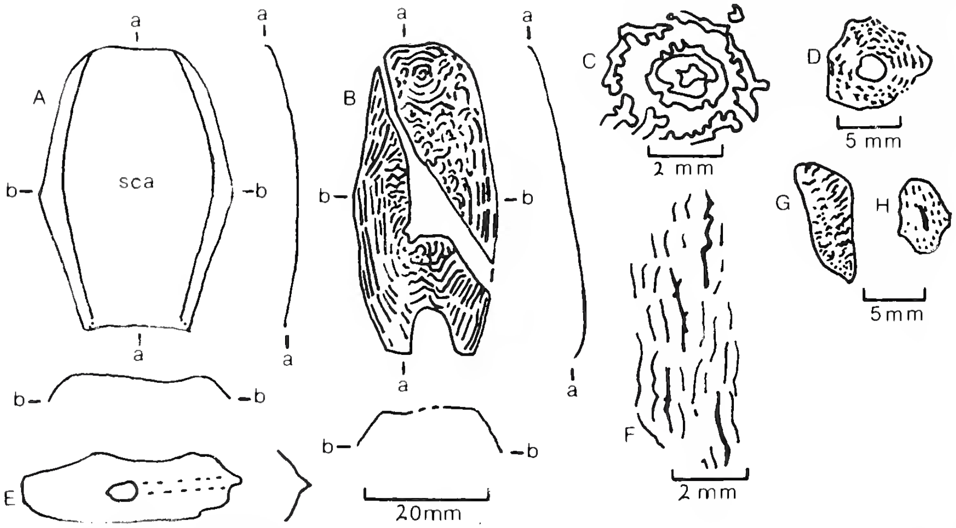
Diagnosis. As for genus.

Description. The dorsal disc is four-sided, vaulted posteriorly, flattened anteriorly, its lateral and posterior edges are gently convex, its anterior edge is indented, and it has slightly raised tubercles at the posterior edge.

A broken plate (Text-fig. 12D) located on the slab BMNH27388, measures 8 × 7 mm, and is perforated medially by a 2 mm wide foramen. Although Dineley and Loeffler (1976) have described distinctive pineal foramina in several Canadian traquairaspidiforms, the large size of the opening shows that this specimen probably represents an orbital plate.

The branchial opening is about 4 mm long × 3 mm wide, postero-laterally facing, and located at about two-fifths along the length, from the front of the branchio-cornual plate (Text-fig. 12E). Fine elongated tubercles run longitudinally behind, and curve across the plate in front of, the branchial opening.

Although the two types of ventral disc could prove to indicate two distinct species, they have identical lateral ornamentation and proportional overlap (Table 3; Text-fig. 12A,B). Also, problems occur with categorizing the other plates into two types. This may indicate that the two types of ventral discs are dimorphic, possibly sexual, examples of the same species. White (1946) showed the segmented longitudinal sensory canals running in association with the longitudinal row of tubercles on each lateral side of ventral disc type 1. Pores show the presence of post-oral canals running on to the anterior half of the smooth central area. These also show the positions of probable ventral medial sensory commissures.



TEXT-FIG. 12. *Traquairaspis campbelli* (Traquair). A, ventral disc type 1, a–a, b–b, lines of cross section, BMNH37379, B, ventral disc type 2, a–a, b–b, lines of cross section, BMNH27037. C, ditto, detail of ornamentation on central area. D, fragmentary orbital plate, p.27388. E, branchio-cornual plate, plus cross section, BMNH43544. F, detail of dorsal disc ornamentation, BMNH43523. G, flank scale, on BMNH43525. H, ridge scale, on BMNH43525. Abbreviation: sca, smooth central area.

On the slab BMNH43525, there are scales of two types. The ridge scales (Text-fig. 12H) lack the pronounced spine or spinal process of phialaspidids, and instead they have a medially placed elongated tubercle. The flank scales (Text-fig. 12G) are very wide compared to those of *P. symondsi*. The most complete ridge scale measures 6 mm long × 4 mm wide and the most complete flank scale measures 5 mm long × 10 mm wide.

Remarks. The morphological similarity and contemporaneity with the Canadian traquairaspidiforms supports Dineley and Loeffler's (1976) assignment of its part of Scotland to the North American Silurian continent. This arrangement is shown by Scotese *et al.* (1985) on their Silurian and Devonian base maps.

Genus RIMASVENTERASPIS nom. nov.

Etymology. Rimas venter, Latin, fissured belly, and *aspis*, Greek, shield.

Type species. ?*Traquairaspis angusta* Denison, 1963.

Remarks. The previous generic name is pre-occupied (*Yukonaspis* Kobayshi, 1936).

Diagnosis. Ventral disc; 80–85 mm long × 35·5 mm wide, with medially notched posterior edge. Ventral smooth central area covers nearly all the disc, is partly subdivided into units which grade into tubercles on antero-lateral edges. Ornament of stellated tubercles became elongated and divided by fine ridges on lateral sides.

Rimasventeraspis angusta (Denison, 1963)

1963 ?*Traquairaspis angusta* Denison, pp. 132–135, figs 78 and 79.
1964 *Yukonaspis angusta* (Denison); Obruchev, p. 63; Stensiö, p. 364, fig. 123A.

Holotype. PU17388, ventral disc.

Type horizon and locality. Silurian, Ludlow/Pridoli, Beaver River, South-eastern Yukon, Canada.

Diagnosis. As for genus, the only known species.

Remarks. A ventral disc fragment described by Dineley and Loeffler (1976) as 'Traquairaspididae indet. Type 1', from the Pridoli of the Delorme Formation, Mackenzie, Canada, may be conspecific with, or closely related to, *R. angusta*.

Discussion. The Traquairaspidinae are readily distinguished from the Phialaspidinae, by a ventral disc with steep sides and a large ventral central region extending to the posterior edge. The ornamentation of small cyclomoriform units suggests a more scale-like dermal arrangement than is found on the phialaspidinids. This, together with the wide flank scales and the absence of a specific pattern of adult growth, would suggest a more primitive condition, in comparison with undifferentiated very scale-like ornamentation and extremely wide, spindly scales of the Ordovician heterostracon *Arandaspis* (Ritchie and Gilbert-Tomlinson 1977).

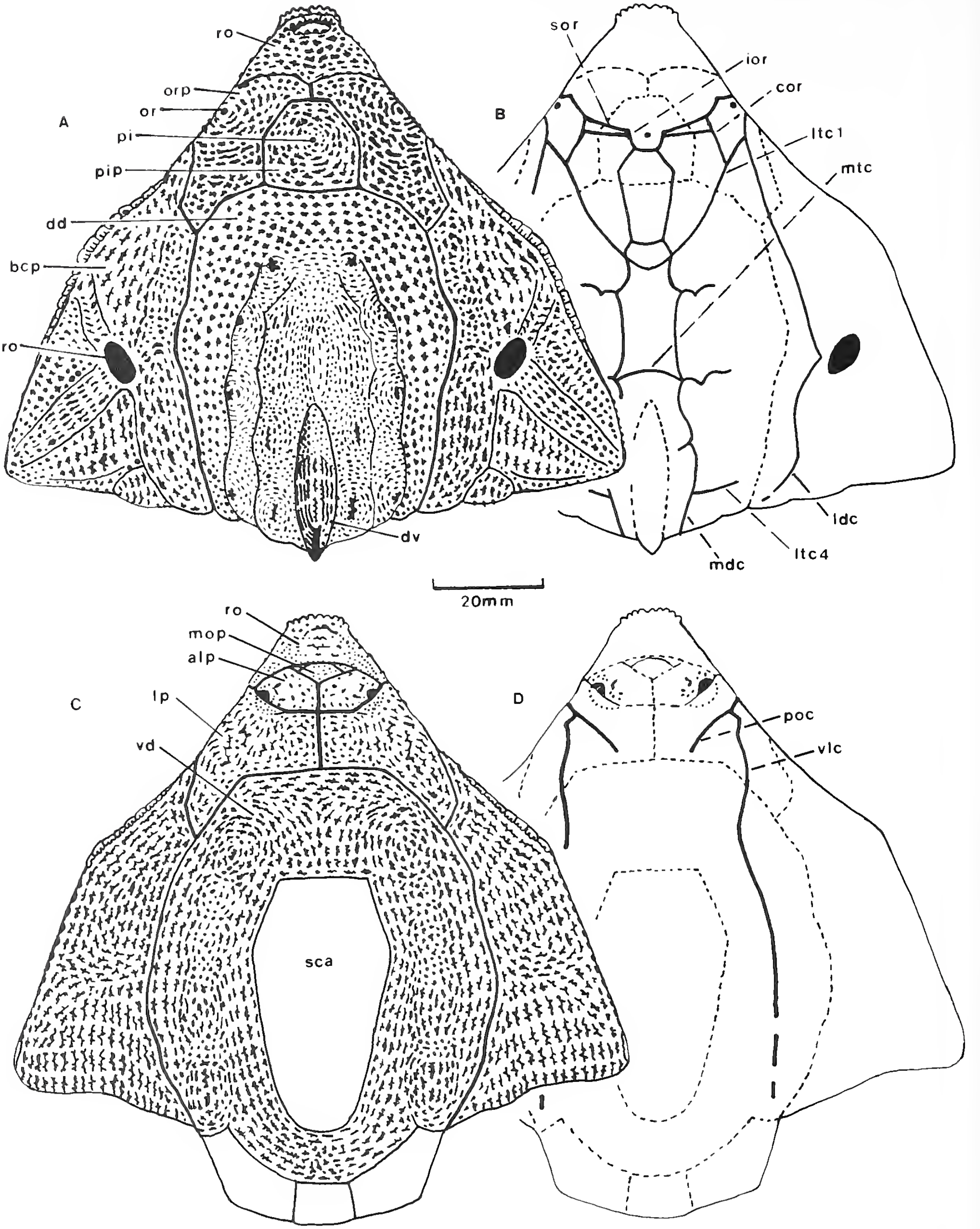
RESTORATION OF PHIALASPIDID CARAPACES

The reconstructions of phialaspidid carapaces (Text-figs 13 and 14) are based upon average measurements (Tables 1 and 2) because of the large proportional range of individual plates, in particular in *P. symondsi*. They have been based upon specimens showing plate fusion, the matching of similarly shaped and sized edges, the similarity of alignment and type of ornament, the matching of the sensory canal system and plate orientation in other heterostracans. Impressions were taken of individual specimens of each component plate, and models were made for both *P. symondsi* and *T. pococki*. This has shown that the plate arrangements in both genera were identical, with the exception of the junction of orbital plates of *P. symondsi* between the rostrum and the pineal plate. In certain regions one edge is often more strongly angled than its corresponding plate margin, suggesting (White 1946) the former presence of small areas of connective tissue.

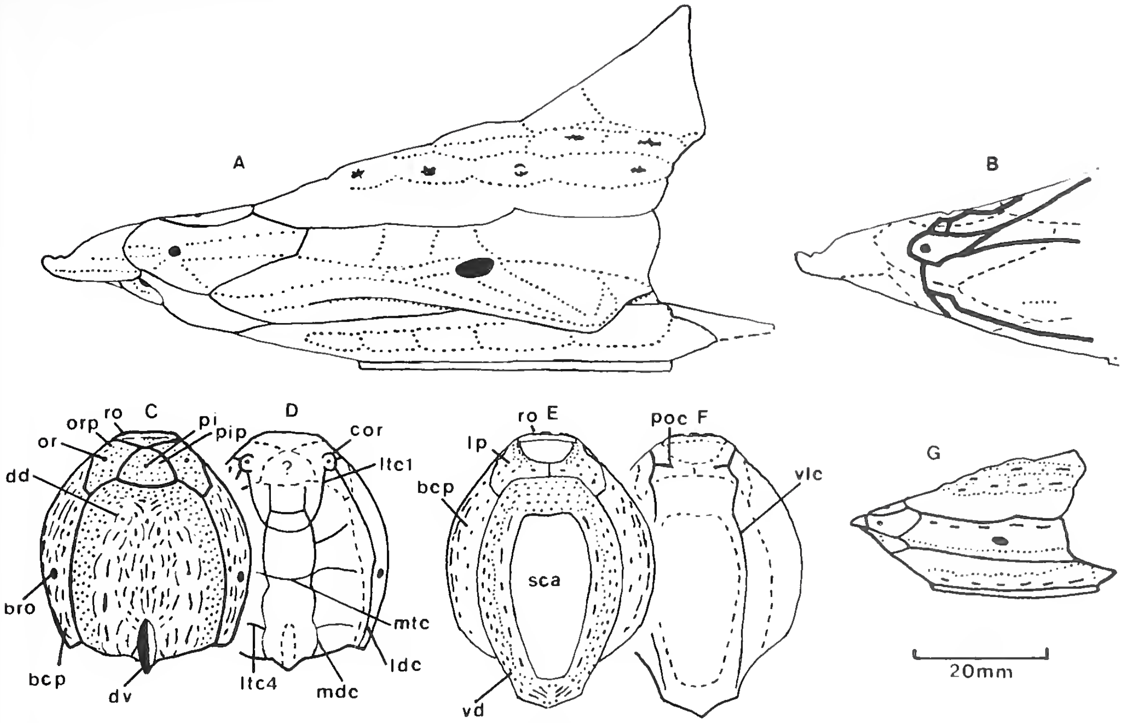
INTERNAL ANATOMY

Impressions of internal organs on the inside of the plates tend to be obscured by impressions of plate growth. Partly because of this, with the exception of the pineal organ, there are no distinguishable impressions of the brain, the semicircular canals, or nasal sacs.

Impressions of the vascular system. The impressions of vessels and possibly nerve fibres, in the basal laminated layer of the exoskeleton, can be seen on many of the specimens of *P. symondsi* from Devil's Hole. These are clearest where radiating from the centres on the interiors of the ventral discs (Text-fig. 10C). The impressions are too incomplete to observe their general ramification, but, at frequent intervals along their lengths, branches leave at right-angles to run through the basal laminated layer into the exoskeleton. As Janvier and Blieck (1979) have observed, these are usually seen as small foramina in the basal laminated layer in heterostracans.



TEXT-FIG. 13. *Phialaspis symondsi* (Lankester), reconstruction of headshield. A,B, dorsal view showing ornamentation and sensory canal system. C,D, ventral view showing ornamentation and sensory canal system. Abbreviations: alp, anterior lateral plate; bcp, branchio-cornual plate; bro, branchial opening; cor, circum-orbital sensory canal; dd, dorsal disc; dv, dorsal vane; ior, inter-orbital sensory canal; ldc, lateral dorsal longitudinal sensory canal; lp, lateral plate; ltc, lateral transverse sensory commissure; mdc, medial dorsal longitudinal sensory canal; mop, median oral plate; mtc, medial transverse sensory commissure; or, orbit; orp, orbital plate; pi, pineal opening; pip, pineal plate; poc, post-oral sensory canal; ro, rostrum; sca, smooth central area; sor, supra-orbital sensory canal; vd, ventral disc; vlc, ventral longitudinal sensory canal.

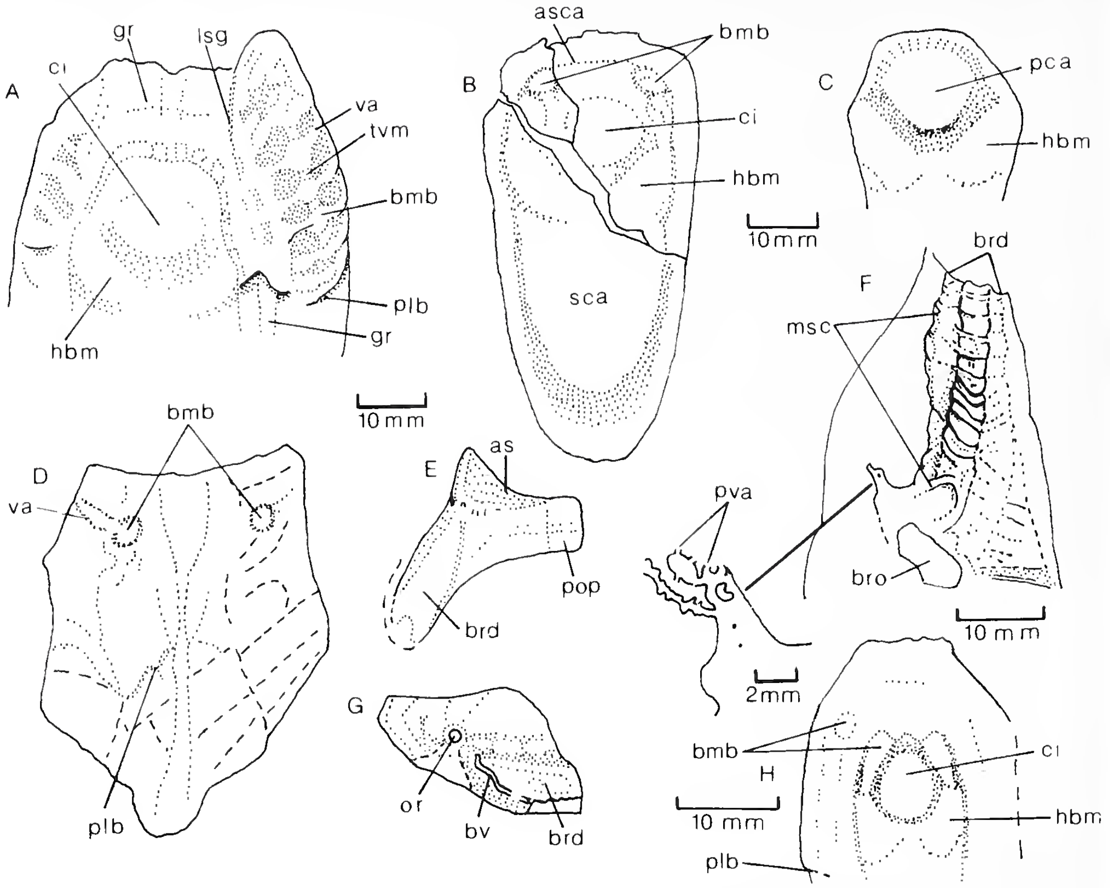


TEXT-FIG. 14. Reconstruction of headshields. A,B, *Phialaspis symondsi* (Lankester); A, lateral view; B, lateral view of anterior portion with sensory canal system. C–G, *Toombsaspis pococki* (White); C,D, dorsal view showing ornamentation and sensory canal system; E,F, ventral view showing ornamentation and sensory canal system; G, lateral view. (See Text-fig. 13 for symbols)

A cone-shaped structure (Text-fig. 15F) found only on the branchio-cornual plate, SHRCM.G08152/1, runs into the exoskeleton of the lateral keel, from near the branchial opening on the branchial duct. It is 6 mm long, 4 mm wide at its base, tapers to 1 mm wide at its tip, and lies at an antero-lateral angle of 50° from the branchial duct. Impressions of vessels adjoin it in places, in particular at the tip.

Branchial structures. The internal, paired and ovate impressions, running in longitudinal rows along heterostracan dorsal and ventral shields, are generally considered to have been made by gill pouches, as originally suggested by Woodward (1891). Stensiö (1958) interpreted longitudinal grooves on the ovate impressions as gill lamellae. Tarlo and Whiting (1965) considered that the paired impressions were made by head somites, which were used to pump the gills. In contrast, Janvier and Blieck (1979) considered that the cephalic somatic musculature was much reduced or absent in the Heterostraci, and its place filled by the branchial apparatus, and that the impressions they observed represented branchial and extrabranchial divisions of the gill pouches, visceral arches with attachment points to the exoskeleton, and an arrangement of nerves closely resembling those found on the branchial regions of the Osteostraci, and the ammocete larva.

White (1946) recognised paired branchial impressions on the anterior parts of a ventral disc of *T. campbelli*. Although he was uncertain about the 'lobes' originally found by Wills (1935), on the smooth, ventral central area of *P. symondsi*, he observed a pattern of rounded ridges on the external surface of that region, in the type specimen of '*Psammosteus anglicus*'. The ventral discs from Devil's Hole show that these impressions run around the shapes of three usually strong and commonly found internal impressions (Text-fig. 15A–C). The most anterior of these is medially



TEXT-FIG. 15. Internal impressions. A–G, *Phialaspis symondsi* (Lankester); A, anterior part of ventral disc showing branchial impressions, SHRCM.G3339; B, immature ventral disc showing branchial impressions, SHRCM.G3527A; C, internal impression of anterior part of ventral smooth central region, SHRCM.G08144; D, imperfect dorsal disc showing branchial impressions, SHRCM.G08144; E, internal view of lateral plate, SHRCM.G08173/2; F, internal view of branchio-cornual plate showing impressions on branchial duct, with detail of vascular structure, SHRCM.G08152/1. G, internal view of orbital plate, SHRCM.G3387. H, *Toombsaspis pococki* (White), anterior of ventral disc showing internal impressions, BU2099. Abbreviations: as, anterior side; asca, anterior edge of smooth central region; bmb, branchial muscle block; brd, branchial duct; bro, branchial opening; bv, blood vessel; ci, central impression; gr, growth ridge; hbm, hypobranchial muscles; lsg, groove for longitudinal sensory canal; msc, muscle scars; or, orbital opening; pca, pre-branchial central impression; plb, posterior limit of branchial region; pop, post-oral process; pva, points of vascular attachment; sca, smooth central area; tvm, transverse muscles; va, visceral arch.

EXPLANATION OF PLATE 6

Figs 1–5. *Phialaspis symondsi* (Lankester), lower Devonian, Welsh Borderland. 1, SHRCM.G3339/1, anterior of internal mould of ventral disc, × 2. 2, SHRCM.G08152/1, internal impression, detail of branchial duct, × 4. 3–5, regions of injury on ventral discs; 3, SHRCM.G08168, external right anterior side of cast, × 1·5; 4, SHRCM.G08195/1, anterior of internal mould, × 1·5; 5, SHRCM.G3302/1, internal anterior of cast, × 1.

1

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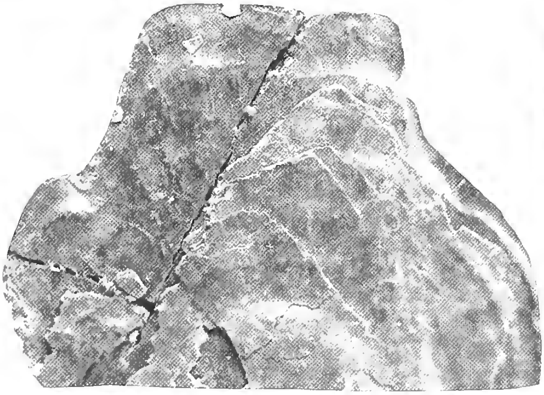

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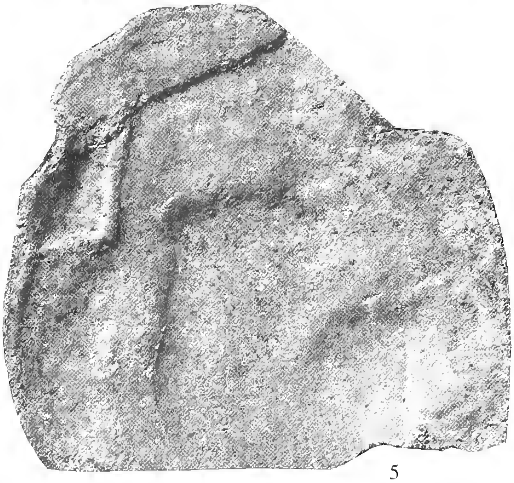


5

TARRANT, *Phialaspis symondsi*

placed and rounded, with an average diameter of 10 mm. At its posterior end, the other impressions form a pair, join medially and fan out antero-laterally on each side, to define the antero-lateral edges of the smooth central region. The average measurements of each of these impressions are about 14 mm long × 7 mm wide.

Branchial impressions can be best seen on the internal mould of the ventral disc, SHRCM.G3339 (Pl. 6, fig. 1; Text-fig. 15A) and these run from the three centrally placed impressions to the antero-lateral edges of the disc. Their posterior edges are clearly defined, and Wills (1935) described these in his specimens, as grooves of indeterminate origin. Lines of beaded, 2 mm wide and raised impressions, divided by lines of pits, are contained on each side within a fan-shaped area. Seven or possibly eight rows are on the left side. On an immature ventral disc SHRCM.G08192 (Text-fig. 15B) the beaded impressions are found closer beneath the internally flattened, antero-lateral corners of the smooth central area, and the two sides are closer together. This resembles the arrangement on the ventral disc of *T. pococki* (Text-fig. 15H). In the dorsal discs, only the distorted specimen SHRCM.G08194 (Text-fig. 15D), shows any branchial impressions, and these are incomplete, but are of the same beaded type as those on the ventral discs.

A row of Y- or U-shaped impressions, running along the dorsal side of the heterostracan branchial duct, and corresponding to the more medially placed branchial impressions, have been interpreted as part of the gill pouches (Kiaer 1930; Kiaer and Heintz 1935; Wills 1935), as impressions marking the positions of branchial pouch openings (Watson 1954; Stensiö 1958, 1964; Tarlo and Whiting 1965; Jarvik 1980), or of visceral arches (Halstead 1982).

The branchial duct in *P. symondsi* can be detected running longitudinally, from below the orbit and the deepest part of the lateral plate, to the branchial opening (Text-fig. 15E,G,F). It is seen most clearly on the branchio-cornual plate SHRCM.G08152/1 (Pl. 6, fig. 2; Text-fig. 15F), where well-defined impressions run transverse across it, along the length of its dorsal side, and most strongly near the branchial opening.

With the possible exception of a large blood vessel on the branchial duct of the orbital plate SHRCM.G3387 (Text-fig. 15G), no obvious impressions of branchial blood vessels or nerves have been detected.

The rows of beaded and depressed impressions undoubtedly represent the positions of visceral arches. The incompleteness and inconsistency of the impressions appears to indicate that the main respiratory movements were endoskeletal, and were mostly made by the branchial region when it was fully expanded. The flexibility and elasticity of the cartilaginous visceral arches would have been an important factor in the extension and contraction of the branchial regions. This explains the rows of beaded impressions, which would represent the positions of branchial muscle plates overlying the visceral arches, and transverse muscles running in between. The large paired impressions, usually found under the smooth ventral central area, have all the appearance of two large hypobranchial muscles, which would have served to raise and lower the branchial regions.

The impressions on the branchial duct of *P. symondsi* could hardly be described as Y- or U-shaped, but rather as bands joining the more medial branchial regions, and swathing the branchial duct. It is unlikely that impressions left by the extrabranchial atria would be found on the lateral branchial region, since they would have been positioned away from the exoskeleton. The impressions in *P. symondsi* appear more like muscle bands, which would have strengthened the internally hollowed and bulky lateral exoskeleton, and could have forced water out through each branchial opening by longitudinal waves of compression, to aid in steering and in controlling pitch and roll.

Janvier and Lund (1983) argued that hypobranchial somatic musculature, found on the myxinoids, anaspids, and to a lesser extent on the lampreys, mobilized the anterior parts of the body, compensating for the lack of paired fins. The same was possible for a juvenile *P. symondsi* at a stage prior to plate growth, as was suggested for the Heterostraci by Tarlo and Whiting (1965). These same muscular contractions could have been used by the adults, to control jet-aided steering and balance.

It seems odd that the Heterostraci did not need paired fins; it seems likely that they had evolved their own substitute. *P. symondsi*, with its streamlined shape, large dorsal and lateral vanes, which indicate an active existence, and its obvious ability to frequent narrow meandering channels, must have manoeuvred more efficiently than is supposed for the Heterostraci, despite its rigid carapace. Water under pressure, forced out of the branchial opening on one side, would push the same side downwards, causing the animal to roll. If this coincided with a yaw in the same direction, the animal would bank, using its wide undersurface to effect a turn. If water was expelled with force from both branchial openings at the same time this would raise the anterior end, which could direct the animal upwards, and slow it down, or stop its forward motion, using the underside as a brake. It seems likely that this proposed method of jet-aided steering could have originally developed as a method of expelling debris from the large and enclosed branchial regions.

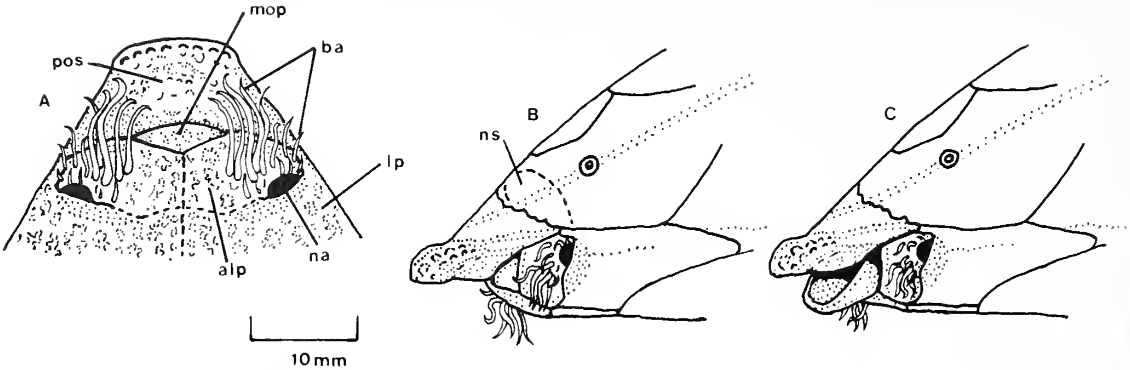
Jarvik (1980) suggested that water expelled through the branchial openings of the pteraspidiforms would have aided the forward movement of the animals to some extent, as is known for modern actinopterygians. As many heterostracans are streamlined, especially so with certain large and advanced pteraspidiforms, it must be assumed that efficient manoeuvrable free-swimming must have been achieved, despite the inflexibility of the carapace. As the branchial openings on most species are directed posteriorly, it is probable that forward movements were jet-aided. The independent expulsion of water to aid in steering in these animals would be less efficient, and would have worked in the opposite way, to the method suggested for *P. symondsi*.

Oral and olfactory apparatus and feeding methods. It has been generally accepted that two circular impressions found internally on the anterior edge of the heterostracan dorsal headshield indicate the position of nasal sacs, as first described by Jaekel (1903). Rostral spaces, medially divided to various degrees, have been found in certain pteraspidiforms (Stensiö 1927, 1932*a*; Heintz 1962; Denison 1964, 1970) and in the cyathaspidid *Torpedaspis* (Broad and Dineley 1973). With the exception of Stensiö (1958, 1964, 1968), who considered that the spaces were filled with cartilage, it has been generally agreed that they would have housed the anterior part of the nasal sacs. Although it has been considered that in some heterostracans the olfactory organ or organs opened into the buccal cavity (White 1935), notches on the anterior edge of the dorsal armour have been described as external nares (Kiaer and Heintz 1932; Watson 1954; Novitskaya 1975). Paired grooves on the rostral under surface of certain pteraspidiforms have been described as olfactory grooves (Zych 1931; Tarlo 1961), or as impressions indicating the position of tentacles (Stensiö 1958; Janvier 1974; Jarvik 1980).

Stensiö (1927, 1958, 1964) was the first to suggest a close affinity between the Myxinoidea and the Heterostraci. In order to do this, he considered that the Heterostraci had a palatosubnasal lamina with 'upper labial plates' against which the oral plates worked, separating the oral cavity from a single medially-placed olfactory organ duct and opening. As no fossil evidence of 'upper labial plates' has been found, Denison (1960), White (1961), Tarlo (1961), Heintz (1962), Halstead (1973), and Novitskaya (1975), disagreed with Stensiö's suggested parts. Stensiö was supported by Jarvik (1980) and by Janvier (1974) who later rejected a close relationship between the two classes, mainly because the Myxinoidea have a single semicircular canal and that the Heterostraci had two (Janvier and Blieck 1979), although they still maintained that the Heterostraci had a 'palatosubnasal lamina', and favoured for most Heterostraci, a medial position for a single olfactory opening, duct and organ. In contrast, Halstead (1973) and Novitskaya (1975) considered that there were two olfactory organs, as in gnathostomes.

The small size and the positions of phialaspidid orbital openings suggest a limited range of vision. Therefore, there must have been a heavy reliance upon well-developed olfactory organs, and possible tactile taste organs, to detect food.

In *P. symondsi*, the folded and contorted under-surface of the back of the rostrum indicates a likely continuation of the external skin that covered the ventral pre-oral surface, and an attachment area for the soft dorsal parts of the mouth. The absence of rostral spaces, the large median oral plate which would have filled the oral cavity medially, plus the likely soft supportive and muscular structures of the oral region, suggest the anterior absence of a palatosubnasal lamina, and a more



TEXT-FIG. 16. *Phialaspis symondsi* (Lankester). A, ventral view of oral region. B, anterior part of head with mouth closed. C, ditto, with mouth open. Abbreviations: alp, anterior lateral plate; ba, barbels; lp, lateral plate; mop, median oral plate; na, narial opening; ns, nasal sac; pos, pre-oral surface.

posteriorly placed olfactory complex, than is accepted on the pteraspidiforms. This indicates lateral positions for possible inhalant openings. It seems that the raised notch on the anterior lateral plate represents an inhalant opening, indicating that *P. symondsi* had paired inhalant olfactory ducts. the foramina surrounding the raised notch might suggest the positions of tactile and possible taste organs. These could possibly be extensions of the olfactory apparatus, as in the myxinoids (Janvier 1974).

The raised notch and foramina may have served to house a large tentacle on each side of the oral cavity. The abrasions on the sides of the median oral plate appear to have been caused by friction against the overlapping anterior lateral plates, indicating that the latter were hinged at their posterior edges, and would have swung open as the median oral plate was extruded. This action, taking into account the shape of the front of the lateral plates, could have been restrained by such tactile organs.

It seems likely that the nasal sacs would have been separated, and have rested under the anterior of the orbital plates. A more medial position for a single olfactory organ would have meant that it had to rest under the telencephalon, which would have involved excessive cranial flexure and where there would have been insufficient room.

Georgieva *et al.* (1979) considered the 'sensory buds' on the barbels of *Myxine glutinosa* resembled the taste buds of the gnathostomes, and Baatrup (1983) described sensory buds in larval lampreys akin to the taste buds of other vertebrates. Therefore, it is feasible that *P. symondsi* may have possessed similar structures, in particular on its tactile organs.

Various suggestions have been made about the oral workings of Heterostraci, particularly the pteraspidiforms and certain cyathaspidiforms. Kiaer (1928) considered that the oral plates bit against the maxillary brim, on the ventral margin of the rostral region. Stensiö (1932) and Janvier (1974) thought that they worked in a myxinoid-like manner. White (1935) considered that the oral plates were connected together by the epidermis, and would have moved down and forwards, to form a scoop or shovel, and Denison (1961) further suggested that the protrusible mouth could have selected and picked up food, including small invertebrates. This could have been aided by inhalant respiratory currents. Dineley and Loeffler (1976) described a large plate in the oral region of *Poraspis* cf. *polaris*, which they interpreted as a large single oral plate used as a scoop.

P. symondsi had far fewer oral components than the pteraspidiforms, and it is inconceivable to imagine its large median oral plate retracting, *Myxine*-fashion, into its gullet. The shape of the median oral plate indicates that it would have worked in the way that White (1935) and Denison (1961) described for the pteraspidiforms. The elongate and convex area on its inner side indicates an attachment area for protractor and retractor muscles, and this suggests that the median oral plate could have, if needed, worked rapidly, snapping shut with force. The smooth edges show that it had no grasping or cutting facilities, although it may have worked against the maxillary flange and pre-oral surface. The size of the oral cavity, surrounded by rigid lateral plates, limited the size of food engulfed. Nevertheless, the oral region of *P. symondsi* has all the appearance of working like an efficient trap, with its scooping median oral plate embraced by anterior lateral plates.

The shape of *P. symondsi*, albeit constricted by an inflexible carapace, has the lines of an active feeder, rather than a sluggish animal swallowing mud and filtering organic substances, as has often been supposed for the Heterostraci (Halstead 1985). The apparent lack of wear on the tip of the median oral plate appears to substantiate this. The small size and structure of the oral region would have prevented total filter feeding in open water. As White (1946) suggested for *Phialaspis*, the smooth ventral central area could have been used as a sliding plane and fulcrum, while the animal wriggled across the surface of the substrate. Taking the dorso-ventrally flattened, and anteriorly heavy, carapace into consideration, plus occasional abrasion observed on the anterior part of the ventral discs and undersurface of the branchio-cornual plates, the crenulated tip of the rostrum, and the ventral position of the oral region, it seems likely that *P. symondsi* was mainly a benthic feeder, rooting in the substrate. This, plus its common and wide occurrence, indicates that it was not a highly specialized feeder, but more of an opportunist, feeding on a wide range of animal and vegetable matter, both dead and alive. Its small mouth rules out any extensive predatory role, but it appears well-equipped to snap up small animals, which it would have disturbed out of the substrate. *T. pococki* had a more evenly vaulted cephalothorax and a short rostrum. Its oral region was more terminal in position (Text-fig. 14E–G), which indicates that it may have fed not so much within the substrate, but more on or possibly somewhat above its surface.

GROWTH AND ONTOGENY

Despite divergent views on heterostracan exoskeletal growth, evidence is patchy. From studies on elasmobranch scales, Ørvig (1951) developed the Lepidomorial Theory, which Stensiö (1958) used to interpret heterostracan exoskeletal growth. This, he considered, was achieved in two ways: (1) cyclomorial growth, in which peripheral concentric growth took place around an initial primordium, and (2) synchronomorial growth, in which calcification was achieved simultaneously, to produce a completed part of the carapace. This was mainly based on the assumption that, once a part of the carapace mineralized, it remained unchanged, and that the mode of growth could be deduced from the form of dentine patterning. However, Dineley and Loeffler (1976) discovered concentric growth impressions in association with synchronomorial dentine patterns in certain cyathaspidiform shields. From this, they argued that the Lepidomorial Theory was not applicable to heterostracan exoskeletal growth, and was only useful to describe cyclomoriform and synchronomoriform ornamental pattern.

An example of phylogenetic heterostracan exoskeletal growth can now be demonstrated, since Elliott (1984) has shown that the pteraspidiforms were derived from the cyathaspidiforms. The superficial layer formed prior to the underlying layers in the cyathaspid (Denision 1964), and during early ontogeny in the pteraspidiforms (Denison 1973; White 1973). The cyathaspidiform shield did not form until the animal had achieved its definitive size (Denison 1964; Dineley and Loeffler 1976), whereas the pteraspidiform shield grew as separate peripheral plates, which fused together at maturity (Heintz 1938; White 1958). This latter process was progressively delayed in later forms (White 1958).

As Dineley and Loeffler (1976) argued, it is likely that the earliest traquairaspidiforms had an undivided dorsal shield, although how this was formed is open to speculation. Nevertheless, to aid in synchronous growth between the animal and its exoskeleton, later forms attained a mode of plate division parallel to the pteraspidiforms.

The orbital, pineal and lateral plates mainly grew cyclomorially by peripheral additions. Much the same could be said about the regions of mature growth in the other major plates. Nevertheless, it would appear likely that some plate remodelling may have been required for fusions and to sustain the proportional vaulting and matching of peripheral plate contacts. Similar speculations have been made about resorption and regrowth in the pteraspidiforms (Halstead 1969; Denison 1973; White 1973), although it has never been demonstrated. However, Tarlo (1965) has shown that certain heterostracans were capable of resorption and regrowth within their middle exoskeletal layers, to aid normal plate enlargement. It would appear that *P. symondsi* was at least capable of using resorption and regrowth to repair broken exoskeletal components (Pl. 6, fig. 5; Text-fig. 10).

Secondary formation of tubercles overlying and replacing primary tubercles has been described in various heterostracans. These formed to repair worn or damaged regions (Tarlo and Tarlo 1965; Tarlo 1965, 1966; Denison 1973), were preceded by resorption rather than wear (Gross 1961), or represented a normal process of growth (Ørvig 1976). In *P. symondsi* the large tubercles overlying smaller tubercles on the lateral edges of the branchio-cornual plates and front part of the rostrum are located on likely regions of abrasion.

Secondary tubercles forming to fill spaces between primary tubercles as a normal part of plate growth have not been described in the heterostracans. Despite this, the evidence of erupting and developing tubercles over the surface of an immature dorsal disc and branchio-cornual plate (Text-figs 2D and 6F) appears to show a ready ability to develop tubercles within the main body of the plates, as part of the general growth. It would seem to follow that this mode of growth of the superficial layer could have been accompanied by resorption and regrowth of the underlying exoskeletal layers.

Tarlo (1962) considered that the traquairaspidiform units grew as isolated tesserae which ultimately fused with the main plates. Although no recognisable isolated tesserae have been found in the beds containing *P. symondsi*, it is conceivable that the units initially developed in Tarlo's suggested fashion, as is apparent from the posterior units on the ventral disc. In certain instances, they may not have fused with the main plates until their growth had ceased. However, evidence of non-cyclomorially arranged developing tubercles in an immature dorsal disc (see Text-fig. 2D) and the small posterior unit in an immature branchio-cornual plate (Text-fig. 6J), suggests that each unit was also capable of growth whilst attached to its neighbouring units and the main plate, thus providing a more or less unified mode of outward plate growth. This contained method of growth could have caused the basal laminated layer to fold inwards at the regions of contact between each unit and their contact with the main plate, thus leaving the internal 'constriction' impressions often observed at the edges of the units (Pl. 1, fig. 2; Pl. 3, fig. 4; Text-figs 2B and 6B). This mode of growth enabled the ontogenetic and phylogenetic development of the folded units forming the dorsal vane. This would suggest that the depressed region in the small dorsal vane (Pl. 1, fig. 3; Text-fig. 3D) may have contained recessed epithelial tissue, in which new tubercles would have formed.

As is evident from the most immature branchio-cornual plates (Pl. 3, figs 1 and 2; Text-fig. 6F–H), the longitudinal units were either isolated or not formed during early ontogeny.

All the known earlier traquairaspidiform rostral plates (Dineley and Loeffler 1976) could be described as an antero-dorsal unit, formed mainly by cyclomorial peripheral growth, with enlarged tubercles at the anterior apex, where it folds to cover the dorsal margin of the oral cavity. However, in *P. symondsi*, there would appear to have been a new centre of cancellous and superficial layer growth within the main body of the plate, forming the 'pre-oral field'.

As Tarlo (1962) suggested, it would appear that the ventral, smooth central region achieved full size and developed an enclosing band of ornamented growth prior to its fusion with, or formation of, the ventral longitudinal units (Pl. 4, fig. 3; Text-fig. 8C). The development of the ventral smooth central region is not seen in any specimens, and its formation is open to speculation. The ventral central ornamentation on certain Canadian Pridolian traquairaspidiforms (Dineley and Loeffler 1976) may illustrate the mode of origin. This grades from the unspecialized ventral tubercles in certain forms, to flattened and broad ventral ornamentation, which approaches the subdivided condition in the ventral smooth central region of *Rimasventeraspis*. The abraded regions in *P. symondsi* show (Text-figs 6D and 8E) broad flattened tubercles like the ventral pattern in the Canadian traquairaspidiforms. Persistent abrasion on the ventral surface of active benthic animals might have triggered selection for a permanently smooth ventral central region. This would have greatly aided movement over the substrate, and might have evolved independently in different lineages. The anomalous and non-abraded ornamentation of the *T. campbelli* Type 2 ventral disc may suggest a different lifestyle, and that the tubercle formation was still inherent, despite the possible ancestral formation of a smooth ventral central region.

The large size range of the phialaspidid adult plates is mainly due to the amount of outer peripheral growth. In the dorsal and ventral discs, growth ridges become more numerous as the region extends. This shows that the animals were capable of growth throughout life. The growth ridges influenced all exoskeletal levels and are seen most clearly as folds in the nasal laminated layer. By folding, the exoskeleton would have been able to have kept itself moulded to the animal, and it appears that the exoskeleton continued to grow for a time. The resulting excess of exoskeletal growth forced the growing edges of a plate downwards, then upwards at the resumption of underlying growth, to form a growth ridge. These corrugations not only mark the rhythmic growth cycles, but would also have strengthened the plates.

The range in proportions of the dorsal vanes, lateral keels, branchial openings, smooth ventral regions, and the number and size of units, appears to have had nothing to do with adult plate growth. No consistent variation can be observed in these parts, and it seems unlikely that they represent species or sexual differences.

From the most immature specimens, it is possible to estimate that *P. symondsi* developed its dermal plates when it was about one-third the length of the mature animal. This shows that an amocoete-like lifestyle was impractical, since a borrowing worm-shaped body, unimpeded by immobilizing plates of a carapace, would have been needed. Regardless of the great size range of orbital and pineal plates, the orbital and pineal openings show a small range in size. This suggests that the orbits and the pineal organ had probably reached full size at the onset of dermal plate development. Also, the posteriorly directed branchial ducts on the juvenile branchio-cornual plates suggest that a relatively large area of the thorax was free of the headshield. At this stage of development, the small animal would have needed sufficient mobility and field of vision to detect and evade predators. It is possible that it first fed upon planktonic organisms in the relative safety of shallow water, and moved into deeper water to consume larger food as it developed its armour and increased in size.

CONCLUSIONS

The morphology of *Phialaspis symondsi* and *Toombsaspis pococki* is sufficiently different from that of *Traquairaspis campbelli*, to necessitate the selection of two families, the Phialaspididae and the Traquairaspididae, within the order Traquairaspidiformes.

Internal impressions on the phialaspidid plates are interpreted as branchial musculature swathing the branchial duct in association with the visceral arches, which could have been used to facilitate jet-aided manoeuvrability to compensate for the lack of paired fins. A conspicuous notch surrounded by foramina in an anterior lateral plate of *P. symondsi* suggests the occurrence of paired olfactory ducts in association with clusters of tactile and taste sensory organs.

Dorsal and lateral swimming stabilizers and a smooth central ventral sliding plane in the Anglo-Welsh phialaspidids, suggests an active and mainly benthic lifestyle. These, their common occurrence, and the workings of the oral region in *P. symondsi*, would imply that these species were probably opportunist feeders, well able to catch and consume small benthic animals.

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THE RHYNCHONELLIDE BRACHIOPOD *EOCOELIA* FROM THE UPPER LLANDOVERY OF IRELAND AND SCOTLAND

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ABSTRACT. Biometrical description of large samples ($N > 300$) of the rhynchonellide brachiopod *Eocoelia* from the Kilbride Formation (upper Telychian) in the west of Ireland and the Lower Camregan Grits (lower Telychian) of the Girvan district, south-west Scotland, suggests the refinement of the stratigraphically important *Eocoelia* lineage in the upper Llandovery. The Irish and Scottish species have previously both been assigned to *Eocoelia curtisi* Ziegler. However, the Girvan population is significantly different from type and topotype specimens from Tortworth and from the Irish material. The Scottish form is accorded separate subspecific status, *Eocoelia curtisi immatura* subsp. nov., whereas the Irish form is included in the nominate subspecies. The Irish and Scottish subspecies are within the upper and lower parts of the range of *E. curtisi* s.l. respectively. Interpolation within the lineage confirms some of the established morphological transpecific trends and may permit more precise correlation within the upper Llandovery.

THE distinctive rhynchonellide brachiopod *Eocoelia* Nikiforova, 1961 (*in* Nikiforova and Andreeva 1961) has been of considerable importance in studies of Silurian benthos. First, the genus is the eponymous component of the widespread *Eocoelia* Community which occupied nearshore environments during the late Llandovery (Ziegler 1965), and secondly the well-documented *Eocoelia* lineage has been effectively used in biostratigraphical correlation within lower Silurian shelly facies (Ziegler 1966). Detailed biometrical analysis of *Eocoelia* from the west of Ireland and south-west Scotland has permitted a significant refinement of the existing Llandovery part of the *Eocoelia* lineage which has some bearing on correlation at and near the base of the Telychian. The analysis, however, confirms some problems in the application of conventional Linnean nomenclature in such gradualist lineages (e.g. Sheldon 1987).

DISTRIBUTION OF *EOCOELIA* IN IRELAND AND SCOTLAND

Eocoelia is relatively widespread throughout the lower Silurian of the Anglo-Welsh area but its distribution is comparatively more localized across Ireland and Scotland. The occurrences in the west of Ireland and Girvan are the only records of the genus from the Midland Valley of Scotland and its Irish equivalent (Text-fig. 1). Two species of *Eocoelia* have been recorded from the West of Ireland. *E. curtisi* Ziegler dominates shell beds within the lower part of the Kilbride Formation along the Silurian outcrop of North Connemara and on the Kilbride Peninsula (Piper 1972); *E. angelini* occurs in the lower Wenlock Lough Muck Formation (*E. sulcata in* Laird and McKerrow 1970). Large new collections of *E. curtisi* have been made from three localities within the lower part of the Kilbride Formation along the Llandovery outcrop in north Connemara as follows: I1, Lough Fee (IGR L 609790); I2, Lettershanbally (IGR L 584836); I3, Lee (IGR L 570 885) (see also Doyle 1989). In the Girvan district, SW Scotland, *Eocoelia* has long been known from the Lower Camregan Grits of the Main Silurian Outcrop, south of the Girvan Valley, in Penwhapple Burn and adjacent areas (Davidson 1867). A. N. H. has made substantial new collections from three localities within the Lower Camregan Grits in the Penwhapple Burn area as follows: S1, (NGR NX 2271 9807); S2, (NGR NX 2230 9799); and S3, (NGR NX 2254 9805); and a new occurrence of the genus is recorded from the Craighead inlier where it occurs with *Pentameroides*.

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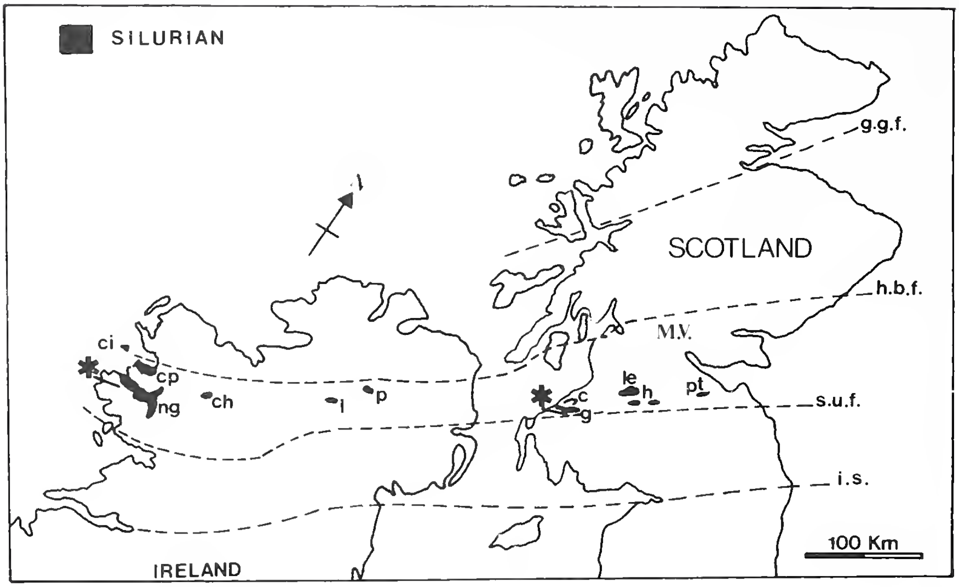


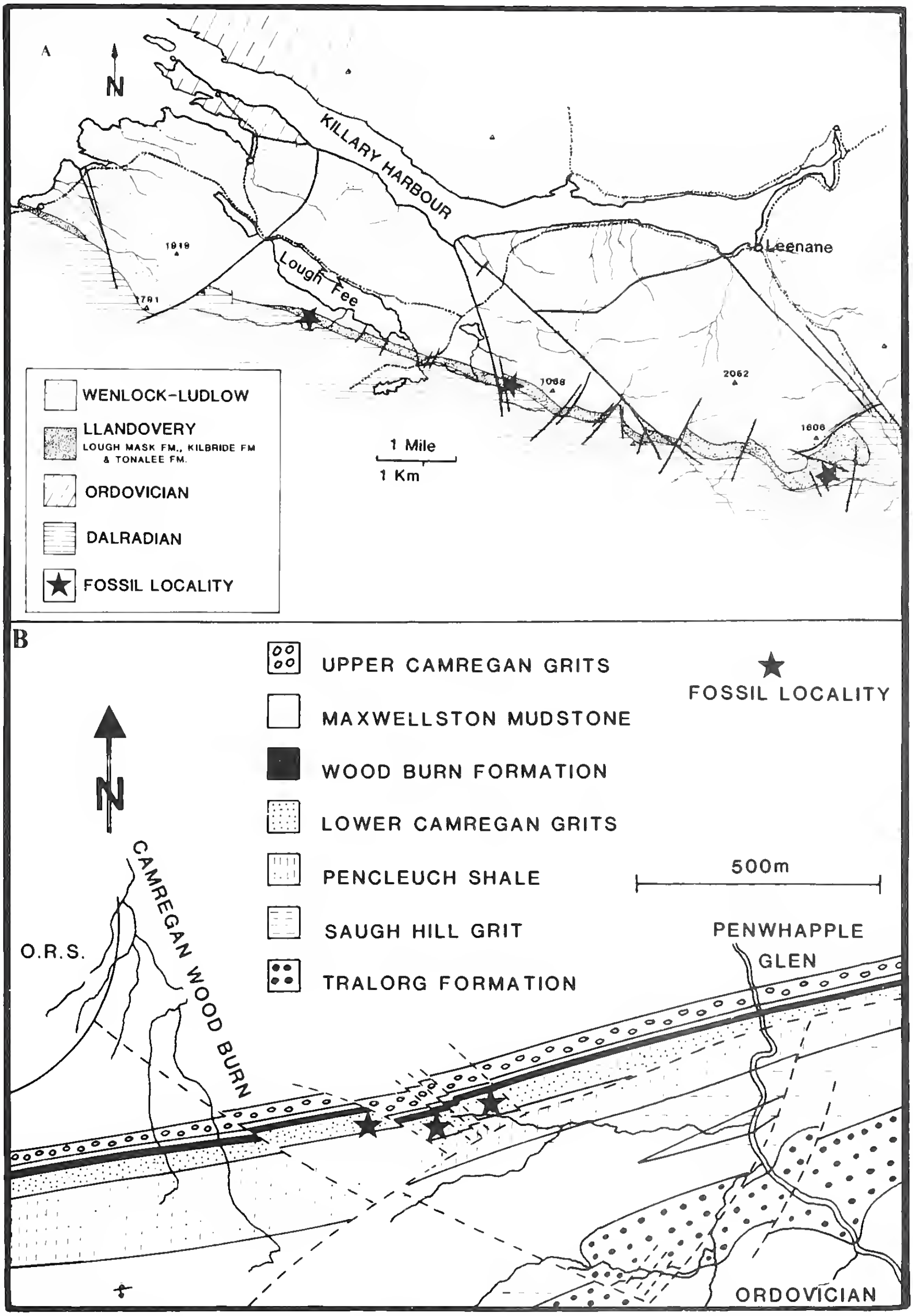
TEXT-FIG. 1. Location of upper Llandovery *Eocoelia* in the Midland Valley of Scotland and its Irish equivalent. Abbreviations: ci, Clare Island; cp, Croagh Patrick; ng, North Galway; ch, Charlestown; l, Lisbellaw; p, Pomeroy; c, Craighead inlier; g, Main Outcrop, Girvan; le, Lesmahagow; h, Hagshaw Hills; pt, Pentland Hills; g.g.f., Great Glen fault; h.b.f., Highland Boundary fault; s.u.f., Southern Upland fault; i.s., putative track of Iapetus suture; M.V., Midland Valley. Occurrence of *Eocoelia* indicated by asterisk.

MORPHOLOGICAL ANALYSIS

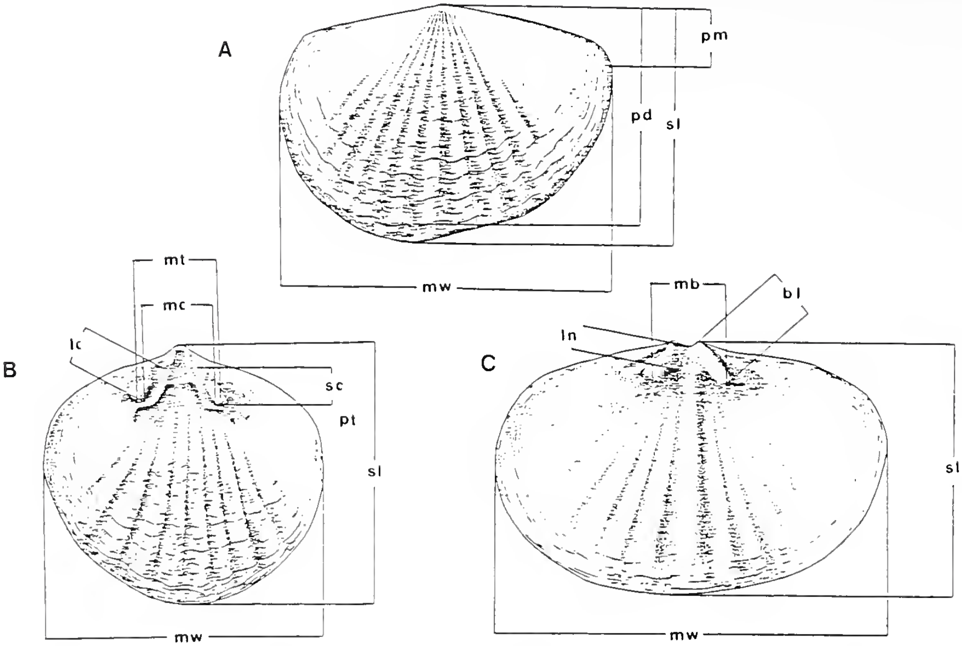
Large samples of *Eocoelia* from Girvan ($N = 342$) and Connemara ($N = 419$) together with a more limited sample of topotype material of *E. curtisi* from the Tortworth inlier were analysed with reference to a set of continuous variates defined below and illustrated on Text-figure 3A–C. The ribbing patterns of all three samples were investigated with the aid of frequency histograms and non-parametric inferential statistics. All graphical and statistical analyses were processed by the PALSTAT package (Harper and Ryan 1987) implemented on a BBC B microcomputer.

Measurements taken (in mm) were sl, sagittal length; mw, maximum width; pm, position of maximum width measured from posterior margin; pt, position of maximum depth measured from posterior margin; pd, position of deflection measured along sagittal length; nr, total number of ribs; lc, total length of crural fossettes; mc, maximum separation of crural fossettes; sc, sagittal length of crural fossettes; mt, maximum separation of teeth; mb, maximum separation of distal ends of the brachiophores; bl, maximum length of brachiophores; ln, length of notothyrial platform. Matrices of sample sizes are shown in Table 1.

Pooled samples both of the brachial and pedicle valve exteriors and interiors from Connemara, Girvan and Tortworth were investigated for size-independent variation within and between samples using the multivariate technique of Principal Component Analysis (PCA); the relationships between the continuous variates, defined above, are described by a correlation matrix from which the appropriate eigenvalues and eigenvectors have been extracted. The rib counts, defined as the total number of costae, for all three samples are displayed as frequency polygons (Text-figs 4 and 5) compared using the non-parametric Kolmogorov–Smirnov test, whilst the rib strength (height/width ratio calculated as a percentage) was similarly investigated by histograms together with parametric and non-parametric inferential statistics (Text-figs 6 and 7). Three features of shell morphology yielded taxonomically significant results: (i) size-independent shape variation between samples of valve exteriors, (ii) the total number of ribs, and (iii) the strength of ribs.



TEXT-FIG. 2. Locality details and stratigraphies for the *Eocoelia*-bearing horizons sampled in the West of Ireland (A) and Girvan, SW Scotland (B).



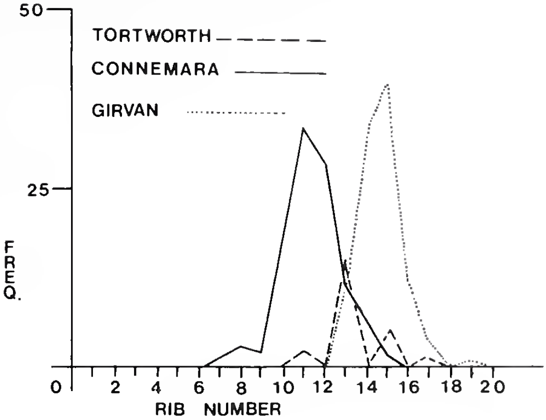
TEXT-FIG. 3. Location of measurements made on the exteriors (A) and ventral (B) and dorsal (C) interiors of *Eocoelia*. Abbreviations and definition of measurements given in text.

TABLE 1. Matrices of sample sizes. Abbreviations: PVE, pedicle valve exterior; PVI, pedicle valve interior; BVE, brachial valve exterior; BVI, brachial valve interior.

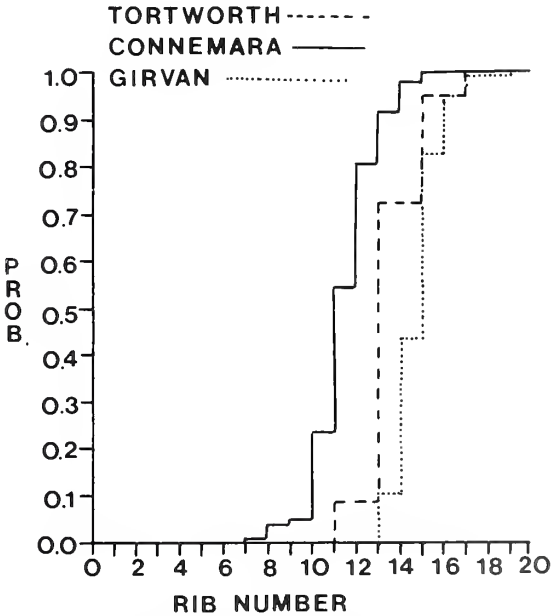
	Girvan				Connemara			
Locality	S1	S2	S3	Total	I1	I2	I3	Total
Valve								
PVE	47	37	33	117	33	35	33	101
PVI	15	11	18	44	32	32	32	96
BVE	33	35	35	102	38	40	33	111
BVI	25	19	35	79	33	45	33	111

Pooled samples of the Connemara, Girvan and Tortworth specimens were investigated by PCA: both pedicle and brachial valve exteriors and interiors were analysed with reference to the variates defined above. The investigation of comparative internal morphology, with reference to the following variates – sl, mw, mb, bl and ln for brachial valves and sl, mw, lc, mc, sc and mt for pedicle valves – yielded no apparent differences between the three samples when each specimen was plotted relative to the second and subsequent (size-independent) eigenvectors. The Irish specimens have markedly larger scores on the first eigenvector, confirming their relatively larger size. However, multivariate examination of the valve exteriors based on the variates sl, mw and pm suggests the samples may also be differentiated with reference to their scores on the second eigenvector (direction cosines: $-0{\cdot}278$, $-0{\cdot}423$ and $0{\cdot}862$) of this analysis; the Irish specimens had significantly lower scores on this eigenvector indicating an outline with a maximum width, on average, nearer the posterior margin (Text-fig. 8).

Significant differences in the rib counts were detected between the Girvan material and the specimens from both Connemara and Tortworth (Text-fig. 5). The Tortworth sample appears to

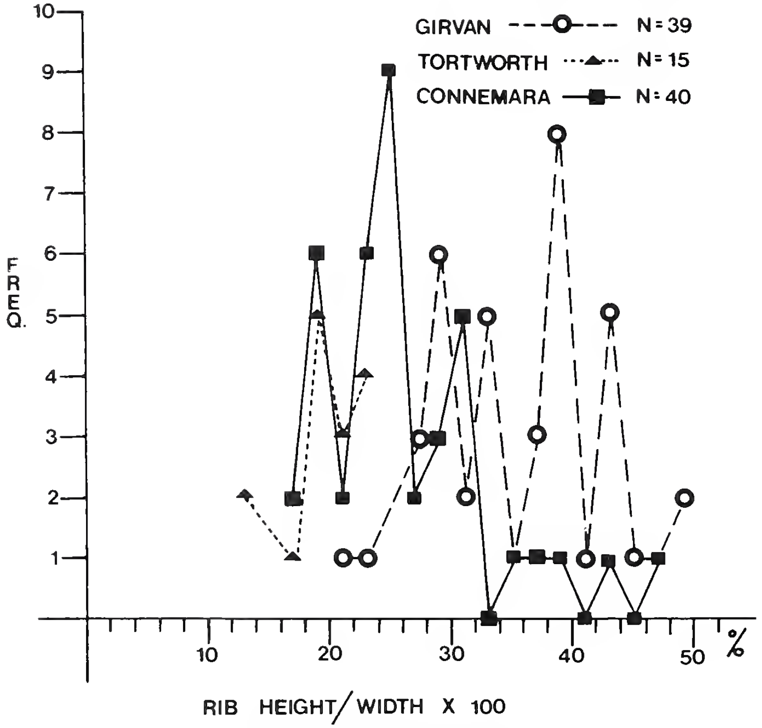


TEXT-FIG. 4. Frequency polygons of total rib numbers on valves of *E. curtisi* from Connemara, Tortworth and Girvan.

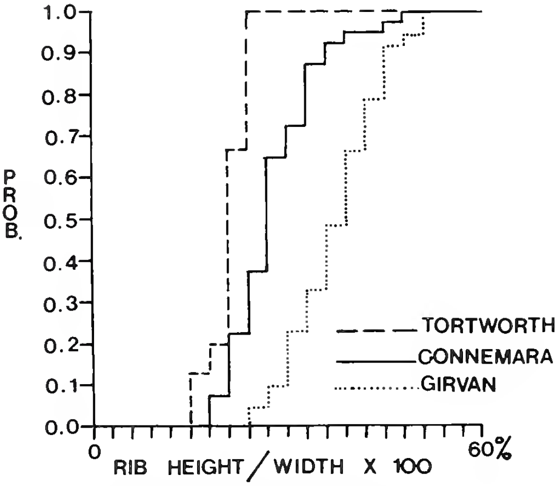


TEXT-FIG. 5. Comparison of the cumulative frequency polygons of the total rib numbers on valves of *E. curtisi* from Connemara, Tortworth and Girvan.

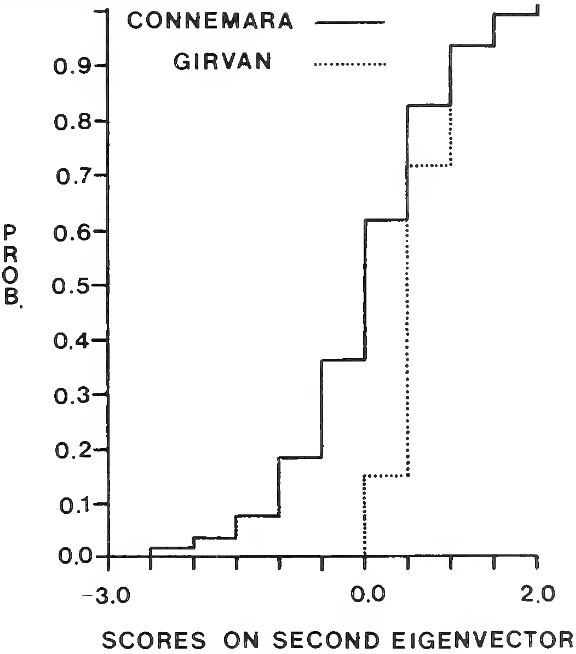
plot between the Irish and Scottish samples on the frequency polygon (Text-fig. 4) and significant differences were detected using the Kolmogorov–Smirnov test (at 1% level) between it and the material from Connemara ($D = 0{\cdot}718$) and Girvan ($D = 0{\cdot}620$). Although Ziegler (1966, p. 530) considered the modal rib density did not appear to behave consistently with time, despite the small samples in many collections, there is in fact a decrease in the number of ribs with time along this part of the lineage: a trend true, in general terms, for the lineage as a whole. Moreover, Ziegler's claim that the stratigraphically older *E. hemisphaerica* (reported modes of 14 and 16) has fewer ribs than *E. intermedia* (reported modes of 16 and 18) is not supported by the data in his table 3. Larger samples and counts of discrete rather than grouped rib numbers may help tighten this putative



TEXT-FIG. 6. Frequency polygons of rib-strength indices for brachial valves of *E. curtisi* from Girvan, Tortworth and Connemara.



TEXT-FIG. 7. Cumulative frequency polygons of rib-strength indices for brachial valves of *E. curtisi* from Girvan, Tortworth and Connemara.



TEXT-FIG. 8. Comparison of the scores on the second eigenvector (direction cosines: $-0{\cdot}278$, $-0{\cdot}423$, $0{\cdot}862$) for a PCA of variates sl, mw and pw for brachial valve exteriors of the Irish and Scottish *Eocoelia*. The Connemara specimens, *E. c. curtisi* have significantly smaller scores on this eigenvector ($D > 0{\cdot}23$ at 1% level – Kolmogorov–Smirnov test).

trend. Sheldon (1987) has shown that evolutionary reversals are possible in otherwise unidirectional evolutionary trends, so it is conceivable that the overall trend of loss of ribs in the *Eocoelia* lineage may be influenced by periods of no loss or possible rib gain.

The rib strength of the taxa from Connemara, Girvan and Tortworth also displayed significant contrasts (Text-figs 6 and 7). Clearly, in view of the probability of some abrasion of the ribs during postmortem transport and modification with compaction, diagenesis and subsequent dissolution, this feature must be treated with some caution. Nevertheless, the clear decrease in rib strength with time is confirmed within the area of the lineage investigated here. Data from the Tortworth (Ziegler 1966, table 6), Connemara and Girvan specimens were compared statistically by F and t tests and the rib strengths of all three samples were compared with those of the stratigraphically older *E. intermedia*. But although the direction of the trend is confirmed, the timing of events within the trend would appear to be slightly retarded. The Irish *Eocoelia* ribs are significantly stronger than those of the nominate subspecies from Tortworth, having rib strengths similar to those of *E. intermedia* from Norbury, whereas the Girvan specimens have rib strengths similar to those of the stratigraphically younger *E. intermedia* from May Hill.

Many of the significant differences may be artefacts of sample comparisons of discrete and spatially isolated segments of a gradualist lineage. Further interpolation within the lineage will clearly strain the existing Linnean framework established for *Eocoelia* and will require a complete revision of its taxonomy or the recognition of categories of lesser rank than the subspecies (see also Sheldon 1987).

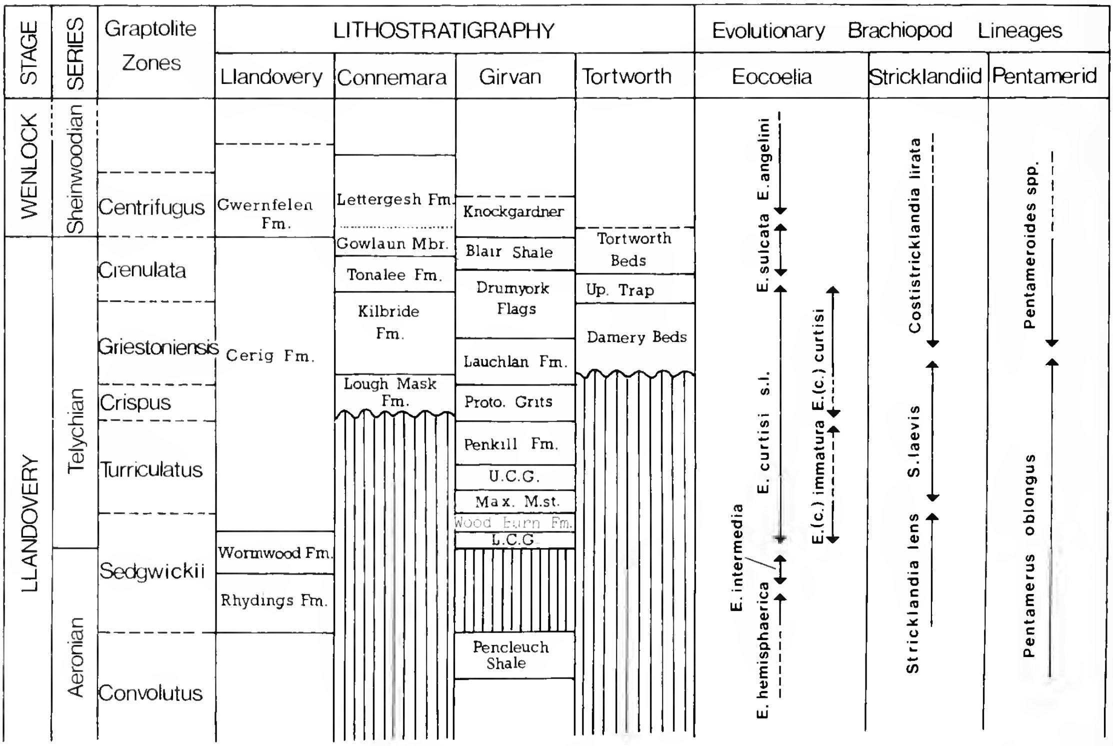
REFINEMENT OF THE *EOCOELIA* LINEAGE

The *Eocoelia* lineage, first established in detail by Ziegler (1966) and later modified by Cocks (1971), has more recently been summarized by Bassett (1984) in its entirety. Cocks *et al.* (1984) have, in revising the type Llandovery Series, documented the lower part of the lineage, summarized on Text-figure 9.

Ziegler (1966) identified a number of clear morphological trends during the phylogeny of *Eocoelia*: (i) strengthening of the articulating mechanisms with a trend towards deeper fossettes, stronger hinge plates and more robust teeth; (ii) reduction in the development of lips and deflections; and (iii) decline in rib strength.

All three samples investigated have well-developed crural fossettes, strong hinge plates and robust teeth, but umbonal chambers are lacking. Although these features are difficult to compare quantitatively, the samples from Girvan, Tortworth and the West of Ireland are consistent with those of *E. curtisi* Ziegler, 1966, confirming their inclusion in that species.

Fourteen percent ($N = 180$) of pedicle and brachial valves from the West of Ireland possessed a deflection whereas only 0·01 % ($N = 220$) of pedicle and brachial valves from Girvan possessed the same feature. Clearly this interpolated trend is contrary to that seen in the lineage as a whole where there is an increase in the development of the deflection and lip. Although Ziegler (1966), in establishing a trend in this aspect of the *Eocoelia* shell, implied that the development of such features is not related to the size of the individual, deflections are in fact most commonly recorded from larger specimens. In the samples investigated by Ziegler (1966), the stratigraphically older species are



TEXT-FIG. 9. Lithostratigraphy of the Connemara, Girvan and Tortworth successions together with brachiopod lineages of correlative value displayed relative to the current graptolite biostratigraphy and chronostratigraphy for relevant parts of the lower Silurian. Abbreviations: L.C.G., Lower Camregan Grits; Max. Mst., Maxwellston Mudstones; U.C.G., Upper Camregan Grits; Proto., Protovirgularia, Up., Upper.

generally larger than those occurring high in the lineage. Ziegler (1966, table 7) reported a total absence of deflections on the shells of *E. curtisi*. The Irish samples are however larger (mean widths of 11·0 and 11·4 mm for dorsal and ventral exteriors, respectively) than the largest mean width (6·68 mm) reported in Ziegler (1966, table 5).

Within the *Eocoelia* lineage (Ziegler 1966) the transition between *E. intermedia* and *E. curtisi* is taken to occur in the lowest part of the *turriculatus* Biozone at a level correlated with the Aeronian/Telychian junction (Cocks *et al.* 1984). Therefore implicit in the definition of this boundary is the coincidence of the base of the *turriculatus* Biozone with the base of the Telychian. In the type area of the Llandovery Series diagnostic graptolite and shelly fossils are rare or absent at and adjacent to the Aeronian/Telychian stratotype boundary. Graptolites are, in fact, absent within the basal part of the Telychian in the type area, although faunas considered diagnostic of the lower half of the *turriculatus* Biozone (Cocks *et al.* 1984, p. 168) are reported 10 km from the stratotype section (Temple 1988, p. 879).

Ascending the type section, *E. curtisi* is first encountered in the lower part of the Cerig Formation, 35 m above the basal Telychian stratotype (Cocks *et al.* 1984, fig. 67), although it is assumed to occur throughout the lower part of the formation (Cocks *et al.* 1984, fig. 69), and thus within the lower part of the *turriculatus* Biozone. Cocks *et al.* (1984, p. 168) considered that the distribution of the relevant *Eocoelia* species and graptolites in the Penwhapple Burn section, near Girvan (Cocks and Toghill 1973) confirmed the coincidence of the base of the Telychian with the base of the *turriculatus* Biozone. However, at Girvan specimens hitherto assigned to *E. curtisi* (see Cocks and Toghill 1973) and assigned here to *E. curtisi inmatura* subsp. nov. occur with *Pentamerus oblongus* in the Lower Camregan Grits. Although Cocks and Toghill (1973) do not record an *in situ* graptolite fauna from the overlying Wood Burn Formation, some slabs in the Gray Collection (British Museum of Natural History) from the Penkill locality suggest a correlation with the upper *sedgwickii* Biozone (Cocks and Toghill 1973, p. 226). The succeeding Maxwellston Mudstones contain a lower *turriculatus* Biozone fauna (Cocks and Toghill 1973, p. 227). Thus, rather than suggesting *E. curtisi* occurs with *turriculatus* Biozone graptolites, the Girvan section indicates a co-occurrence with graptolites of the *sedgwickii* Biozone.

Clearly, the lack of graptolite control across the Aeronian/Telychian boundary stratotype invites correlation of the upper part of the Wormwood Formation with either the lower *turriculatus* or upper *sedgwickii* biozones. However, in the absence of more equivocal faunal control in the type area, the faunal data from Girvan suggest the base of the Telychian may be better correlated with a horizon within the upper part of the notional *sedgwickii* Biozone. Moreover there is a gap of some 65 m in the *Eocoelia* lineage between the last occurrence of *E. intermedia* in the upper part of the Wormwood Formation and the first occurrence of *E. curtisi* in the Cerig Formation. If the lineage is as cosmopolitan as previous and current documentation suggests, then forms similar to *E. c. inmatura*, together with graptolites of the *sedgwickii* Biozone, might be expected within this faunal hiatus.

North of the Girvan valley, in the Craighead inlier Cocks and Toghill (1973) have documented the co-occurrence of *E. curtisi* (*E. c. inmatura* herein) and *Pentamerus oblongus* within the Lower Camregan Grits. Extension of the pit in Craigfin Wood (Cocks and Toghill 1973, p. 217) has yielded a new fauna in higher strata: a species of *Pentameroides* occurs with a number of poorly preserved specimens assigned, on the basis of their outlines and rib numbers, to *E.* cf. *curtisi curtisi*. Poor exposure and complex faulting in this part of the inlier presents considerable stratigraphical difficulties; nevertheless, the co-occurrence of *Pentameroides* and a form approximating to the nominate subspecies of *E. curtisi* supports the correlations presented in Text-figure 9.

In the west of Ireland, *E. curtisi curtisi* occurs with *Costistricklandia lirata* and *Pentameroides* within the Kilbride Formation, presumably near the top of its range. Although no diagnostic fossils are present in the overlying Tonalee Formation (Doyle *et al.* 1990) the succeeding Benbeg Mudstones contain *crenulata* Biozone graptolites (Rickards 1973).

SYSTEMATIC PALAEONTOLOGY

Family TRIGONIRHYNCHIIDAE McLaren, 1965

Genus EOCOELIA Nikiforova, 1961 (*in* Nikiforova and Andreeva 1961)

Remarks. Cocks (1978, p. 149) transferred *Eocoelia* from its traditional site within the Atrypida, on the basis of an undescribed species of *Eocoelia*, from the Idwian (Aeronian) of Shropshire, with similarities to *Rostricellula*.

Eocoelia curtisi curtisi Ziegler, 1966

Text-fig. 10

1867 *Atrypa? hemisphaerica* J. de C. Sowerby; Davidson, p. 136 (*pars*), pl. 13, figs 24–30*a*, non fig. 23.

1966 *Eocoelia curtisi* Ziegler, p. 537 (*pars*), pl. 83, figs 7 and 8; pl. 84, figs 12–17.

Holotype. OUM C3241; an internal mould of a pedicle valve from the Damery Beds (Telychian) of the Tortworth Inlier, Gloucestershire; pl. 84, figs 15, 16, 17 of Ziegler 1966.

Material. About 200 pedicle valves and 200 brachial valves, all virtually complete, none conjoined.

Diagnosis. Nominate subspecies of *E. curtisi* with 7–16 (mode 11 – Connemara or 12 – Tortworth) strong ribs developed on brachial valve exteriors; maximum width posterior to midvalve length and rib strengths about one-quarter.

Description

Exterior. Medium-sized, planoconvex valves of transversely subquadrate to subelliptical outline with maximum width posterior to mid-valve length. Hinge line about four-fifths maximum width, cardinal extremities obtuse and rounded. Pedicle valve about three-quarters as long as wide and about one-quarter as deep as long; anterior and lateral profiles convex medianly but in later growth stages growth vectors change to produce anterolateral flattening. Maximum depth occurs between one-fifth and two-fifths valve length. Brachial valve about three-quarters as long as wide, essentially flat with faint median sulcus and flatly convex flanks. Deflection of valve profile present on 14% of pedicle and brachial valves ($N = 180$). Ornament of strong costae of evenly rounded, semicircular profile, numbering 7–15 on 1, 3, 2, 20, 34, 29, 12, 7, 2 valves and with mean (variance) rib strength (height/width * 100) of 26·4 (43·5) for 40 brachial valves; costae subdued or absent posterolaterally. Concentric growth lines absent posteriorly but accentuated anteriorly.

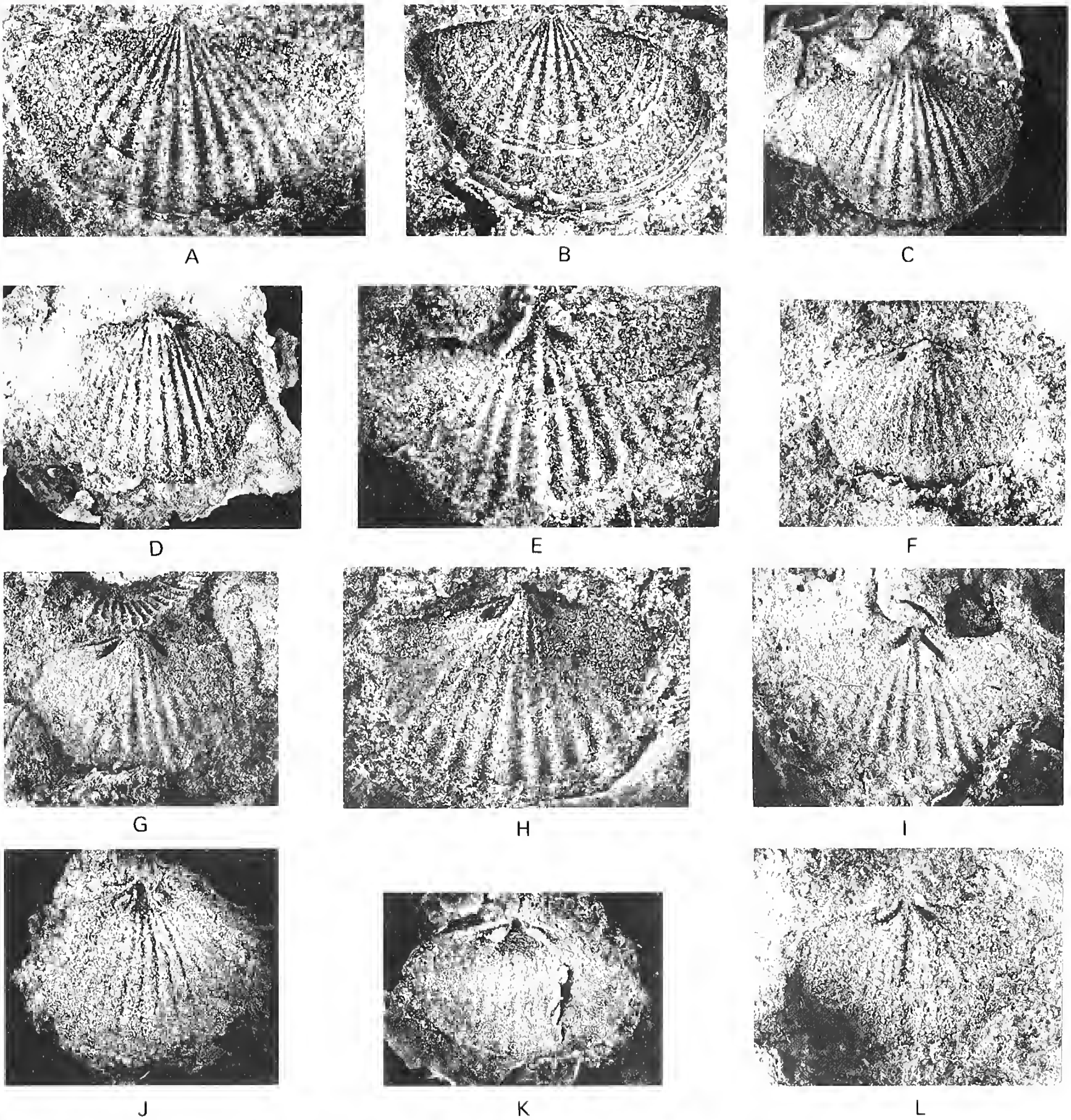
Ventral interior. Delthyrial chamber moderately deep with faint pedicle callist rarely developed in posterior half. Large cyrtomatodont teeth, oval to triangular in dorsal view with rounded anterior surfaces. Dental plates absent; teeth attached directly to shell wall. Large fossettes cut deeply into medial face of teeth extending into shell wall. Muscle scars not impressed.

Dorsal interior. Socket plates large, well developed, almost rectangular in ventral view, diverging at 55–75 degrees and supported posteriorly on broad, raised notothyrial platform; cardinal process very rarely ($< 1\%$) present. Sockets deep, conical and widely divergent. Median ridge arising anterior to notothyrial platform and extending to about one-half valve length. Muscle scars feebly impressed.

Measurements and statistics

Brachial valve exteriors

Variates	sl	mw	pm
Sample size	110	111	110
Means	7·71	11·0	2·46
Variance–covariance matrix	2·29	2·87	0·58
		4·92	0·74
			0·39



TEXT-FIG. 10. *Eocoelia curtisi curtisi* Ziegler, from the lower part of the Kilbride Formation, north Connemara. A, external mould of brachial valve, JMM Br1000, × 3. B, external mould of brachial valve, JMM Br1001, × 3. C, latex cast of pedicle valve exterior, JMM Br1002, × 2. D, latex cast of pedicle valve exterior, JMM Br1003, × 3. E, latex cast of brachial valve interior, JMM Br1004, × 3. F, internal mould of pedicle valve, JMM Br1005, × 2. G, internal mould of pedicle valve, JMM Br1006, × 2. H, internal mould of pedicle valve, JMM Br1007, × 3. I, internal mould of brachial valve, JMM Br1008, × 3. J, latex cast of pedicle valve interior, JMM Br1009, × 3. K, latex cast of pedicle valve interior, JMM Br1010, × 3. L, internal mould of brachial valve, JMM Br1011, × 3.

Brachial valve interiors

Variates	sl	mw	mb	bl	ln
Sample size	104	105	111	111	111
Means	8·00	10·8	1·90	1·24	0·82
Variance–covariance matrix	1·76	2·47	0·43	0·23	0·13
		4·98	0·81	0·40	0·19
			0·20	0·09	0·04
				0·08	0·04
					0·03

Pedicle valve exteriors

Variates	sl	mw	pm	pt
Sample size	98	100	100	100
Means	8·06	11·4	2·82	2·80
Variance–covariance matrix	2·06	2·17	0·61	0·57
		3·95	0·66	0·53
			0·32	0·23
				0·36

Pedicle valve interiors

Variates	sl	mw	lc	mc	sc	mt
Sample size	96	96	96	96	96	96
Means	8·21	11·2	1·23	2·01	1·09	2·42
Variance–covariance matrix	2·07	2·37	0·18	0·35	0·21	0·44
		4·02	0·25	0·54	0·26	0·65
			0·06	0·06	0·04	0·07
				0·15	0·06	0·16
					0·05	0·07
						0·21

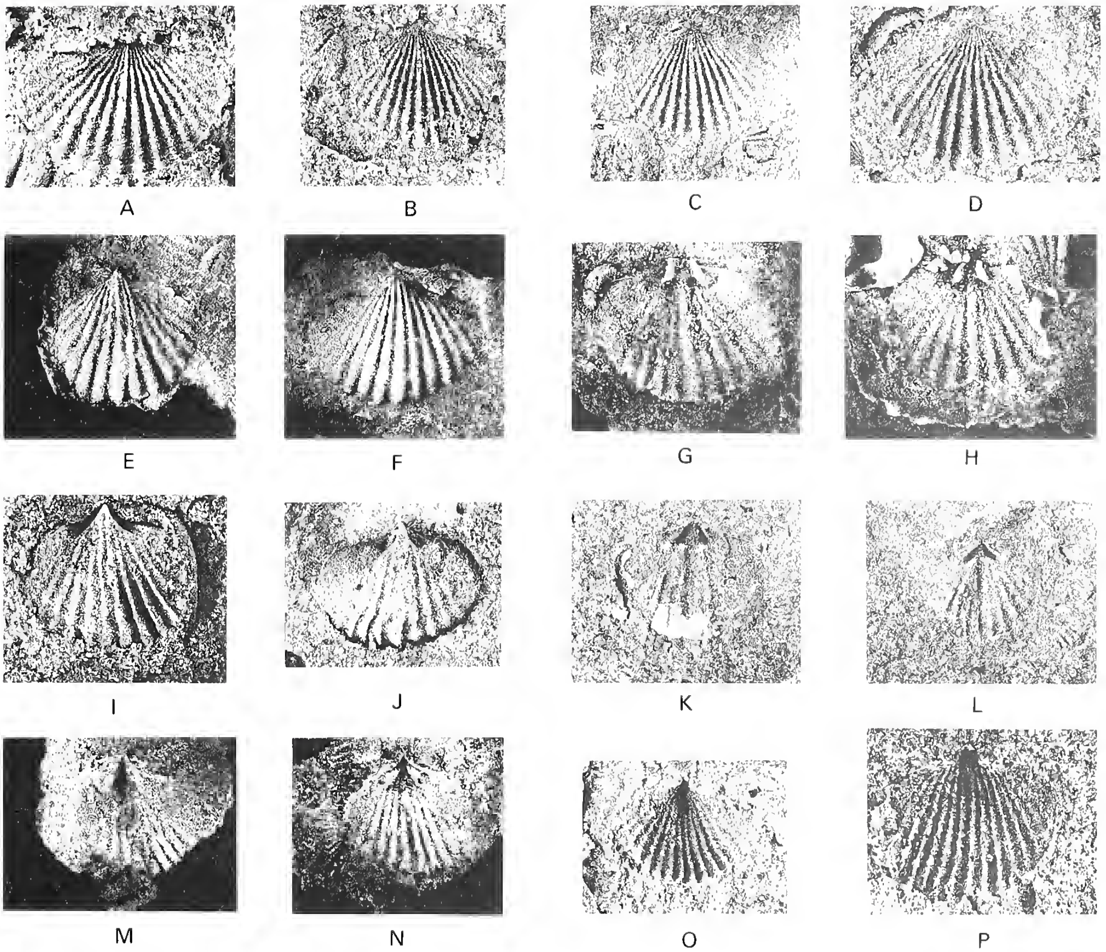
Remarks. The description of *E. curtisi curtisi*, presented here, is based exclusively on material from the lower part of the Kilbride Formation, which crops out along the northern margin of Connemara. The Irish specimens are considered morphologically identical to the type and topotype material of the nominate subspecies from Tortworth except for the development of the ribs. The ribbing strengths of the various *E. curtisi* morphs have been discussed above. However, analysis of the rib counts of the Tortworth and Connemara specimens presents taxonomic difficulties. A Kolmogorov–Smirnov test, as noted above, indicates a significant difference between the two frequency distributions. The Irish material has a modal value of 11 ribs, that from Tortworth has a mode of 12. However, the sample from Tortworth is disproportionately smaller than that from Ireland. Moreover it is probable that the Connemara specimens are from slightly younger horizons than those from Tortworth, thus confirming the trend of decreasing rib number with decreasing time. Since the Irish *E. curtisi* agrees in all other aspects with the nominate subspecies it is not separated on the basis only of the modal rib counts. However, it may be suggested the two represent chronological morphs of the same subspecies which a more rigorous investigation of more material may confirm or reject.

Eocoelia curtisi Ziegler, 1966 *immatura* subsp. nov.

Text-fig. 11

1867 *Atrypa? hemisphaerica* J. de C. Sowerby; Davidson, p. 136 (pars), pl. 13, figs 25, 27–30.
1973 *Eocoelia curtisi* Ziegler; Cocks and Toghill, p. 225, pl. 3, figs 1–3.

Name. Latin *immatura*, youthful morphological characteristics.



TEXT-FIG. 11. *Eocoelia curtisi* Ziegler *immatura* subsp. nov. from the Lower Camregan Grits, Penwhapple Burn, Girvan. A, external mould of brachial valve, JMM Br1012, × 3. B, external mould of brachial valve, JMM Br1013, × 2. C, external mould of brachial valve, JMM Br1014, × 2. D, external mould of brachial valve, JMM Br1015, × 3. E, latex cast of pedicle valve exterior, JMM Br1016, × 2. F, latex cast of pedicle valve exterior, JMM Br1017, × 3. G, latex cast of brachial valve interior, JMM Br1018, × 3. H, latex cast of brachial valve interior, JMM Br1019, × 2. I, internal mould of pedicle valve, JMM Br1020, × 2. J, internal mould of pedicle valve, JMM Br1021, × 2. K, internal mould of brachial valve, JMM Br1022, × 2. L, internal mould of brachial valve, JMM Br1023, × 2. M, latex cast of pedicle valve interior, JMM Br1024, × 2. N, latex cast of pedicle valve interior, JMM Br1025, × 2. O, External mould of pedicle valve, JMM Br1026, × 2. P, external mould of pedicle valve, JMM Br1027, × 3. All type and figured specimens are deposited in the James Mitchell Museum, University College Galway, Ireland.

Holotype. JMM Br1020; an internal mould of a pedicle valve from the Lower Camregan Grits, Penwhapple Burn, Girvan, SW Scotland.

Material. About 150 pedicle valves and about 180 brachial valves, all virtually complete, none conjoined.

Diagnosis. Small subspecies of *E. curtisi* with 13–19 (mode 15) strong ribs developed on brachial valve exteriors; maximum width at or near midvalve length and rib strength of about one-third.

Description

Exterior. Small, planoconvex valves of subquadrate outline with maximum width at or near mid-valve length. Hinge line about three-quarters maximum width with obtusely rounded cardinal extremities. Pedicle valve about four-fifths as long as wide and about one-quarter as deep as long with maximum depth at about one-third valve length. Delthyrium relatively wide and open. Brachial valve about four-fifths as long as wide and essentially flat. Ventral and dorsal interareas obsolete. Ornament of relatively strong ribs of evenly rounded profile developed over entire valve surface and numbering 13–19 on 11, 34, 40, 13, 4, 0, 1 valves with rib strength of mean (variance) 35·8 (47·4) for 38 brachial valves.

Ventral interior. Relatively deep delthyrial chamber flanked by large cyrtomatodont teeth, oval in dorsal view with rounded anterior surfaces; dental plates absent. Dental fossettes cut deeply into medial face of teeth. Muscle scars not impressed.

Dorsal interior. Large, robust socket plates, elongately rectangular in ventral view and distal parts anteriorly divergent on low notothyrial platform. Deep, divergent conical sockets. Broad median ridge extending anteriorly from margin of notothyrial platform. Muscle scars not impressed.

Measurements and statistics

Brachial valve exteriors

Variates	sl	mw	pm
Sample size	103	103	103
Means	5·61	6·90	2·30
Variance–covariance matrix	0·73	0·80	0·24
		1·14	0·32
			0·14

Brachial valve interiors

Variates	sl	mw	mb	nl	ln
Sample size	79	79	79	79	79
Means	5·84	7·08	1·44	1·14	0·54
Variance–covariance matrix	0·82	1·00	0·12	0·10	0·05
		1·49	0·19	0·15	0·08
			0·08	0·04	0·01
				0·04	0·01
					0·01

Pedicle valve exteriors

Variates	sl	mw	pm	pd	pt
Sample size	117	117	117	117	117
Means	5·35	6·47	2·34	1·62	13·2
Variance–covariance matrix	2·19	1·94	0·72	0·52	0·39
		2·86	0·91	0·69	0·66
			0·43	0·27	0·18
				0·28	0·10
					1·53

Pedicle valve interiors

Variates	sl	mw	lc	mc	sc	mt
Sample size	44	44	44	44	44	44
Means	5·99	6·80	0·66	1·33	0·55	1·55

Variance–covariance matrix	0·89	0·71	0·13	0·12	0·09	0·14
		0·61	0·10	0·11	0·07	0·13
			0·03	0·02	0·02	0·02
				0·03	0·01	0·03
					0·02	0·01
						0·04

Remarks. The Scottish material, hitherto referred to *E. curtisi* by Cocks and Toghill (1973), differs in two main respects from the nominate subspecies. First the maximum width is at or near the mid-valve length and secondly it has more and stronger ribs. Taken together, the morphological contrasts may be interpreted as specific differences; however, the Girvan, Connemara and Tortworth samples are characterized by well-developed crural fossettes, strong hinge plates and robust teeth; umbonal chambers are absent. This association of characteristics conventionally describes *E. curtisi*; the differences, therefore, are accorded only subspecific status.

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THE ROLE OF PREDATION IN THE EVOLUTION OF CEMENTATION IN BIVALVES

by ELIZABETH M. HARPER

ABSTRACT. The independent appearance of many taxa of cementing bivalves during the early Mesozoic coincided with the marked increase in predation pressure described by Vermeij (1977, 1987). A causal link is implied by experimental work in which predators were offered the choice of byssate or cemented bivalve prey: cementation confers a significant selective advantage by inhibiting manipulability. The example illustrates the potential value to palaeontology of studies in behavioural ecology.

EPIFAUNAL bivalves attach to the substratum by two means: cementation by one valve or, more commonly, anchorage by byssal threads produced by the foot. Yonge (1962) believed that most, if not all, living bivalves possess a byssus in the larval stage, and that this structure was retained in some adults, for example the Mytilacea and the Arcacea, by neoteny. It would seem that the cemented habit in bivalves was evolved in stocks already possessing a functional adult byssus; indeed most living cementing bivalves, e.g. the Spondylidae and *Hinnites*, pass through a byssate stage in early ontogeny.

EXPERIMENTAL WORK

A series of experiments was designed to establish the relative vulnerability to predation of byssate and cemented bivalve prey. Asteroid and crustacean predators were offered the choice of bivalves attached both bysally and by cementation. *Mytilus edulis* was used for both prey types, so that any preference expressed would be due to mode of attachment only, rather than on the basis of different nutritional quality. Mussels with established byssal threads were collected intertidally in Dunstaffnage Bay, Oban, and cementation was simulated using an epoxy resin (Araldite Rapid – Ciba Geigy) to fix the shell by one valve to large blocks of substratum. These 'cemented' *Mytilus* fed normally and even produced superfluous byssus threads and hence behaved identically to the byssate individuals. Many byssate individuals were daubed with epoxy in order to monitor any inhibitory effect on predator behaviour (e.g. masking metabolite cues from the prey): no such effect was apparent. Treated and untreated specimens were eaten in equal proportions.

The experiments were run in outdoor running seawater tanks (1·5 × 0·8 m), each set up with a random distribution of the byssate and 'cemented' prey. A number of individuals of *Asterias rubens*, *Cancer pagurus* or *Carcinus maenas* were introduced into each tank, having previously been starved for at least four days. Regular observations were made on the feeding behaviour of the predators and any prey item taken was replaced with an identically attached individual. Hence the relative numbers of prey types were held constant.

RESULTS

If cemented and byssate prey were indistinguishable to predators, one might expect that they would be eaten in the proportions in which they occur in the tank (the null hypothesis). The results were in fact very different: a much higher proportion of prey taken was byssate (see Text-fig. 1). Chi-squared one-sample analysis of these results reveals that the preference for byssate prey over cemented was highly significant, rejecting the null hypothesis for *Asterias* and *Cancer* ($P \ll 0{\cdot}001$),

PREDATOR	TOTAL NO. PREY TAKEN	NO. EXPECTED OF EACH	NO. BYSSATE EATEN	NO. CEMENTED EATEN	NO. PULLED FREE	P
Asterias rubens	121	60.5	95	11	15	<<0.001
Cancer pagurus	132	66	96	7	29	<<0.001
Carcinus maenas	27	13.5	19	4	4	<0.05

TEXT-FIG. 1. Experimental results of choice trials. Statistical analyses by χ^2. (All 'cemented' prey that was pulled free was treated in analysis as 'cemented'.) The null hypothesis that byssate and cemented prey are equally vulnerable to predation is rejected for *Asterias* and *Cancer* ($P \ll 0{\cdot}001$), and for *Carcinus* ($P < 0{\cdot}05$). The use of the binomial test confirms this significance.

and for *Carcinus* ($P < 0{\cdot}05$). Binomial analysis was also employed in order to verify the significance and produced similarly significant levels. A number of the 'cemented' bivalves were pulled free and eaten. Statistically these were treated by including them with eaten 'cemented' prey, as Feifarek (1987) has demonstrated that during predation in the natural environment the right valve of *Spondylus americanus* may be broken from the substratum.

Observations showed that prey types were encountered according to their relative numbers in the tank. Rejection of 'cemented' prey was rapid, the predator moving on to tackle another individual. Some of the predators employed unorthodox methods of entry into the 'cemented' mussels. Instead of chipping in the manner described by Elner and Hughes (1978), *Carcinus* snipped along the ligament between the two valves without damaging them; *Asterias* broke valves in three instances. Hancock (1965) has also reported *Asterias* damaging mussels that were difficult to open.

DISCUSSION

Both predator groups used in this experiment need to manipulate their prey to feed. Chelate crustaceans use the chelae to assess the size of their prey and to locate weak points for attack. The rock lobster *Jasus edwardsii*, feeding on detached *Ostrea lutraria*, first holds the prey vertically and then reverses it (Hickman 1972). In the tanks both *Cancer* and *Carcinus* were observed to grasp the prey items in the master chela, rotating them around before pressure was applied to crush the valves. *Asterias* encountering *Mytilus* moves the prey so that the ventral valve margins of the shell are opposite its own oral region. Asteroids feed on bivalves by pulling the two valves apart with their arms and inserting stomach lobes in between the valves into the prey, thus feeding extraorally. In assuming the classic humped feeding position, the asteroid pulls the bivalve into a vertical position.

These results may be interpreted in terms of optimal foraging, as described by Krebs and Davies (1981), whereby predators are shown to choose prey that maximize the energy yield against energy expended to locate and subjugate it. The 'cemented' bivalves are less easy to manipulate than are those attached by a flexible byssus. Hence the effort required, and thus energy expended by the predator, is higher when dealing with cemented prey. Where byssate and cemented prey have the same energy yield, it is preferable in terms of net energy gain for the predator to take the former. The unorthodox feeding methods employed by some of the *Asterias* and *Carcinus* may reflect a 'learned' response to deal with suboptimal prey. Cunningham (1983) reported that *Carcinus maenas* has a very rapid learning ability of altered feeding tactics.

Anecdotal evidence from the literature further demonstrates the advantages conferred by cementation on predation resistance. *Octopus dolfleini* prefers not to eat the cemented rock scallop, *Hinnites giganteus*, despite its presence close to the den (Hartwick *et al.* 1981), whilst crustaceans feeding on oyster spat are able to take a larger size of detached than of attached spat (Mackenzie 1970; Elner and Lavoie 1983). Feifarek (1987) detached *Spondylus americanus* and transplanted them into shallow water where they suffered a much higher mortality than on the reef. He attributed this to a higher vulnerability in shallow water, but it may equally well be interpreted as due to the decreased predator resistance of loss of attachment. Seastars cause extensive damage to oyster shellfisheries (Galtsoff and Loosanoff 1939), but commercially spat are detached at a very early stage in order to facilitate their harvest.

Although it is clearly possible for predators to eat cemented bivalves, the difficulty of manipulation compared with byssally attached bivalves, with their more flexible attachment, makes them less energetically favourable prey. It would seem intuitively obvious that a bivalve which becomes adapted for cementation will be selected for over evolutionary time.

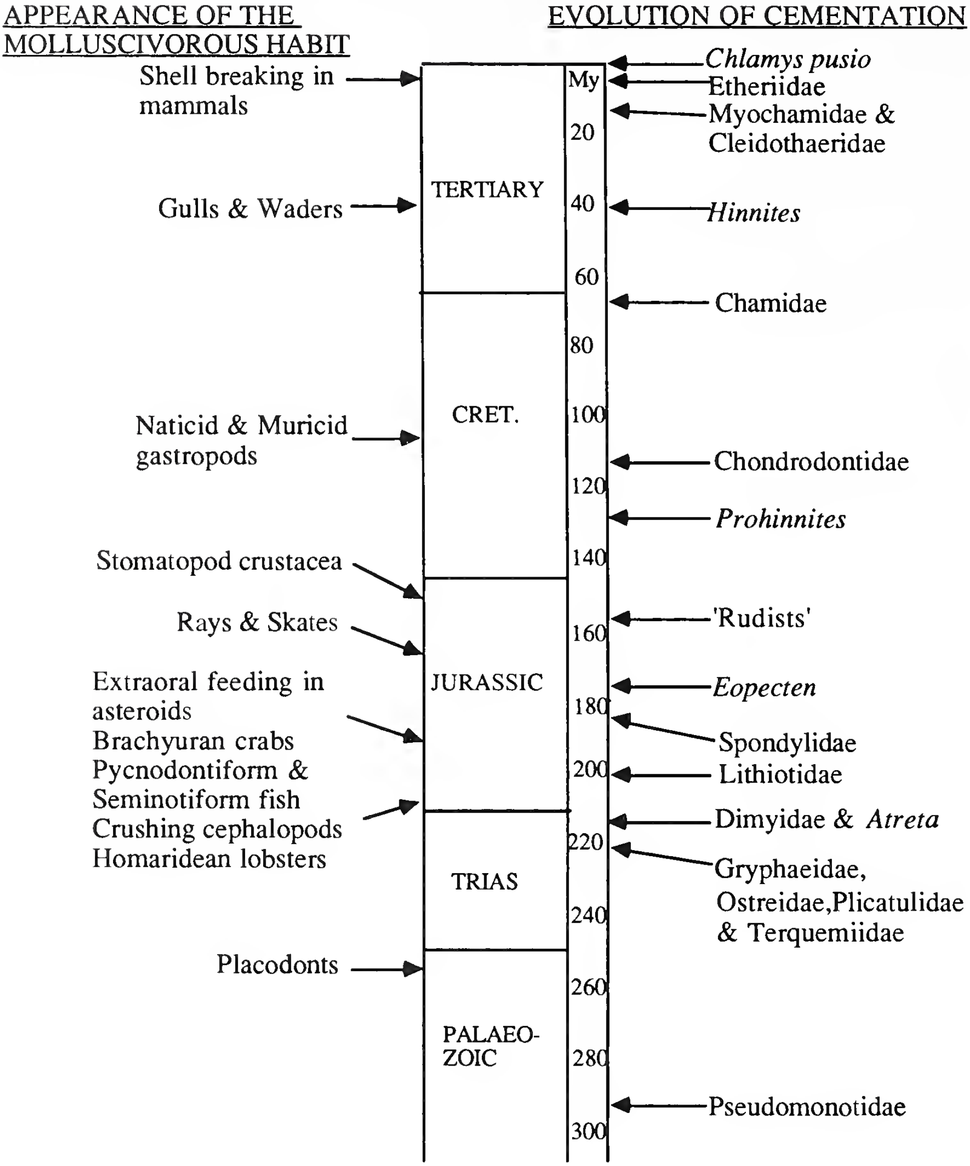
IMPLICATIONS IN THE FOSSIL RECORD

More than sixteen families of bivalved mollusc have or have had representatives with the ability to cement to a hard substratum. Adaptations for cementation appear to have been acquired independently in over twenty clades. Some groups, for example the oysters and the extinct Mesozoic rudists, have been extremely successful over geological time.

It is traditional to view the habit as an adaptation to life in a turbulent environment (Kauffman 1969; Yonge 1979). Many byssate bivalve groups, however, also flourish in high energy conditions, for example the Mytilacea and the Arcacea. Udhayakumar and Karande (1986) have surveyed the relative strength of adhesion of various biofouling organisms: they showed that the force required to break the byssus threads of *Mytilus edulis* is considerably more per unit area than to sunder *Crassostrea cuculata*. Byssate attachment has a number of other advantages: the possibility of seasonally variable attachment strength (Price 1980); voluntary detachment for mobility, including secondary larval settlement; and the ability to reattach if dislodged accidentally. Cementation denies such advantages. In fact Nicol (1978) can determine 'no compelling reason to become shell cemented'.

Apart from the Pseudomonotidae, some of which cemented in the Carboniferous (Newell and Boyd 1972), cementation in bivalves is a post-Palaeozoic habit. Text-figure 2 shows the temporal distribution of the first independent appearance of the cementing bivalve groups. It appears that the Late Triassic and Jurassic were key times in the evolution of the habit. This pattern is strikingly coincidental with the first appearance of many durivorous predator groups during the Mesozoic and their diversification thereafter – the Mesozoic Marine Revolution (MMR) described by Vermeij (1977, 1987). Palmer (1982) has postulated that the increase in shelly epifauna in hardground communities during the Mesozoic may be due to predation rather than to scour resistance. Many notable molluscivores appeared during that time (see also Text-fig. 2). Although asteroid echinoderms evolved in the early Palaeozoic, it is suggested that it was not until the Triassic/Jurassic that the asteroids attained the suckered tube feet and the eversible stomach necessary for extraoral feeding (Blake 1981; Gale 1987). This ability to feed by prising the valves apart and extruding the stomach into the prey has made the modern seastars most voracious molluscivores. Palaeozoic seastars undoubtedly fed upon bivalved molluscs (Clark 1912), but probably only as scavengers.

Gastropods, in particular the drilling muricids and naticids, are also notable molluscivores. Drilling in these gastropod groups becomes prevalent from the Albian and Aptian stages of the Cretaceous (Taylor, Cleevely and Morris 1983; Taylor, Morris and Taylor 1986), although Fürsich



TEXT-FIG. 2. On the right is the temporal distribution of the first appearance of the cemented habit in independent clades in which the habit has been acquired, based on Skelton *et al.* (in press), figure 5 (data derived from personal records, Newell (1969), Waller (1978), Stenzel (1971), Skelton (1978), Newell and Boyd (1972) and Kennedy *et al.* (1970)). The timing of the appearance of various molluscivorous groups over geological time is plotted to the left, modified from Vermeij (1987).

and Jablonski (1984) report possible gastropod drill holes from the Triassic. It seems likely that this mode of predation which involves little manipulation would not be hampered by cementation. Their appearance in the Cretaceous is not marked by further proliferation of cemented taxa. However, further experiments are envisaged using gastropod predators.

The experimental evidence described here gives a strong suggestion that the appearance of many cemented bivalve taxa at the same time as the start of the MMR may not be coincidental. If not a primary selective force favouring the initiation of cementation, then the increased predator resistance must at least have been a valuable evolutionary spin-off.

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MORPHOLOGIC PATTERNS OF DIVERSIFICATION: EXAMPLES FROM TRILOBITES

by MIKE FOOTE

ABSTRACT. The morphologic diversification of the Trilobita is investigated using a Fourier description of the cranidia of Cambrian and Ordovician trilobites from North America. Morphologic diversity increases from the Early Cambrian to the Middle Ordovician, but does not correlate well with patterns of generic or familial diversity. Suprageneric taxa of trilobites are shown objectively to represent morphotypes. Morphologic dispersion among suprageneric taxa and the distinctness of these taxa both increase from the Cambrian to the Ordovician. This result agrees with patterns based on hypostomal morphology (Whittington 1988*a*, 1988*b*), and therefore is not an artifact of using cranidial morphology. These patterns are caused by the origination of new higher taxa, not evolution within established higher taxa. Higher taxa tend to retain the same morphology once established, rather than diverging gradually. In this respect, higher taxa may be said to have sudden origins. The origination of higher taxa may be linked to the opening of new adaptive zones, particularly in the Early Ordovician, following widespread extinctions of trilobites.

THE fossil record clearly indicates that evolutionary change is not evenly distributed over time, but is concentrated in episodes of evolutionary radiation. For the Metazoa at least, the early Phanerozoic represents the most important of these episodes. Yet, despite its significance, a limited number of approaches has been used to study this great diversification, most notably the analysis of taxonomic data (e.g. Valentine 1969; Erwin *et al.* 1987). Often implicit in the analysis of diversification by 'taxon counting' is the assumption either that morphologic diversity can be measured by taxonomic diversity, or that the number of taxa reflects the number of objectively discernible morphotypes. Valentine (1969), for example, used the assumption that the separation among groups at a higher taxonomic level usually represents a larger morphological divergence than that among groups at a lower level in order to draw conclusions about community evolution from temporal patterns in the appearance of groups at various taxonomic levels.

Although we know that taxonomic data and morphologic data often correlate, taxonomic and morphologic approaches are not simply redundant. If taxa are consistently defined, then taxonomic data can tell us about the number of biological units at a given time. But if we want to know the nature of these units, how they originate, and how they evolve once established, morphologic data are clearly necessary. Since form represents the raw data of palaeobiology, it is important to document significant events in the history of life from the standpoint of morphology.

Because the events of the early Phanerozoic diversification are concentrated in the Cambrian and Ordovician, documenting patterns of morphologic evolution associated with this radiation requires a well preserved fossil group that is diverse and abundant during these two periods. Trilobites are clearly the group of choice. Although all skeletonized metazoan phyla were present by the Ordovician, some 75 % of known Cambrian species were trilobites, while trilobites account for 23 % of described Ordovician species (Raup 1976). It is the availability of trilobites, rather than any intrinsic property such as complexity, that makes them useful for a case study in diversification.

This study has two principal objectives: (1) to document patterns of morphologic diversification in the Trilobita during the Cambrian and Ordovician; and (2) to investigate morphologic dispersion within and among suprageneric taxa of trilobites in order to determine the taxonomic level(s) at which morphologic diversification is concentrated. Although this paper focuses on trilobites, it is important to keep in mind that trilobites provide only a case study. It is hoped that the results may yield generalizations regarding morphologic radiation when compared to information from other

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groups of organisms and other times in the history of life. Finally, while it is interesting and important to test hypotheses regarding the mechanisms and processes of evolution, it is necessary first to document patterns in the rough. Therefore, although ecological and evolutionary processes will be discussed, the following analysis is largely exploratory.

MATERIAL AND METHODS

Morphometric foundations

The consideration of large scale patterns of morphologic evolution requires the establishment of a morphospace, i.e., a multidimensional lattice of morphologic variables in which biological forms can be consistently and objectively represented. This involves (1) the selection of an aspect of form (some part or parts of an organism), and (2) the means to describe that aspect of form. The choice of the part of the organism can be justified *a priori* (e.g. on ecological grounds), or *a posteriori* if patterns of evolution based on a subset of morphology seem concordant with patterns based on a more extensive set of features.

For trilobites, the cranidium is appropriate for studying large scale evolutionary patterns. First, it is well preserved and recognizable through time and across nearly all taxonomic lines. Second, it has ecological significance in reflecting the size and orientation of sensory structures such as eyes, the style of moulting, and the attachment of feeding appendages. Finally, as shown below, patterns of cranidial evolution are concordant with subjective assessments based on gross morphology and hypostomal morphology.

For nearly all Cambrian and Ordovician trilobites the cranidium, or 'central dorsal portion of cephalon bounded laterally by facial sutures' (Harrington *et al.* 1959, p. O119), is easy to define and identify. In the case of marginal sutures (e.g. Harpina, Trinucleacea), the lateral bounds of the cranidium can be identified with the lateral margin of the cephalon. In some cases (e.g. some Phacopina) the facial suture is not functional, but can nevertheless be identified. The only difficulty is with olenellids and some agnostids, which lack a facial suture. For purposes of this study the cranidium in such cases is operationally defined as if the cephalon were bounded by a marginal suture. This solution is purely operational, and the 'cranidium' so defined obviously does not have the same biologic significance as the true cranidium. However, it seems that for these few exceptions it would be unwise to discard an otherwise very useful morphologic system. It should be noted that in the material studied here, the number of specimens without a definable cranidium is less than 2% of the total sample size. Therefore it is unlikely *a priori* that this limitation would present a serious bias.

The question of morphologic evolution involves the consideration of descent with modification. Therefore, one would ideally hope to recognize a set of homologous points or features that could be defined consistently among all taxa at all times. This is difficult for the cranidium, since the suture is a continuous feature with few discrete landmarks. (Of course, the cranidial midline or axis itself is an homologous feature, but it alone enables little morphologic description.) Considering other parts of the trilobite, homologous points may be identified within certain groups, for example fringe pits in trinucleids (Hughes 1970) and tubercles in encrinurids (Temple and Tripp 1979). However, such features cannot be meaningfully recognized on all trilobites.

Given this limitation, it is necessary to consider shape *per se*. This has previously been done by considering sets of linear measures (e.g. Ashton and Rowell 1975; Rowell *et al.* 1982), but the utility of this approach generally depends on restricting the analysis to a relatively small group of trilobites. In this study, shape was quantified by a Fourier description of the closed curve that represents the projected outline of the cranidium. (This method is discussed in detail elsewhere (Foote 1989*b*), and only cursory treatment will be given here.) The glabella is an important biological feature, since it reflects cephalic segmentation, as well as a feature of much utility in taxonomy. However, because it is often difficult to identify consistently, especially in many of the taxa with effaced forms, such as the Asaphacea and Scutelluina, its morphology was not considered in this study. The cranidium provides only a limited assessment of morphology, but it is necessary to sacrifice detail for the sake of a large-scale analysis such as that presented here (see also Raup 1966, 1967). For work at finer scales, the cranidial outline would clearly be inadequate.

Following the guidelines of Shaw (1957, p. 194), the cranidium is placed in a standard orientation. The cranidium is oriented with the palpebral lobe horizontal, or, if this is not possible, with the axial furrows horizontal. With very convex forms, the chord to the palpebral lobe or axial furrow is used to orient the specimen (Shaw 1957, p. 194). This standard orientation allows comparison among many diverse forms, and thus has an advantage over using presumed 'life positions', which vary from group to group, and in many cases are not known. The error associated with orienting and measuring specimens has been shown to be small (Foote 1989*b*).

The projected outlines of cranidia were drawn with a microscope and camera lucida. These drawings were digitized electronically and shape analysis was performed on the stored images. As described previously (Foote 1989*b*), 12 Fourier coefficients contain approximately 99% of the shape information contained in the cranidial outline. These 12 coefficients were used as morphometric variables, forming the basis of a 12-dimensional morphospace. In order to allow equal weighting of the variables, the data were standardized as $x' = (x - \bar{x})/s$, where x is the original variate, $\bar{x}$ is its mean, s is its standard deviation, and x' is the standardized variate. (Standardization was used rather than a method such as the percent-range or percent-maximum transformation, since these last two techniques rely on single, observed values [minimum and/or maximum]. In general, such single values are expected to be more heavily influenced by sampling than statistics of the entire population [the mean and standard deviation], which are more reliably determined.) In order to allow comparisons among stratigraphic intervals, all data were standardized at once, rather than one interval at a time.

The definition of the outline is straightforward except when there are spines. These spines are of two types: (1) those that actually form part of the cranidial margin (e.g. genal spines), and (2) those that are not part of the margin but project out over it (e.g. occipital spines). Because spines of the first type actually define the outline of the cranidium, these were included. Spines of the second type were excluded, i.e., the cranidial outline was drawn as if the projecting spine were not present.

Scope

This study is limited to the Cambrian and Ordovician. Although the Cambrian and Ordovician do not contain the major part of the total diversity of most skeletonized marine animals, the majority of trilobite abundance and diversity is concentrated in these two periods. Thus, the analysis documents most of the evolutionary history of the trilobites.

To keep the study tractable, sampling is limited to North America. Because the analysis presented here is at a coarse taxonomic level (the evolutionary history of superfamilies, suborders and orders), biogeographic changes alone would seem unlikely, *a priori*, to cause the observed patterns. It is shown below that patterns documented with North American trilobites are concordant with those subjectively determined using more extensive distributions of trilobites. Therefore, with respect to the questions addressed here, the evolution of trilobites in North America is representative of the evolution of the global trilobite fauna. Furthermore, but perhaps less significantly, provinciality appears not to change from the Cambrian to the Ordovician (Valentine *et al.* 1978; Sepkoski 1988).

Preservation

Trilobites are frequently sheared, compressed, or crushed. For character recognition, identification, and systematics, this may not present severe problems. However, morphometric analysis requires either undistorted material or material that is consistently distorted. Consistent distortion is nearly impossible to obtain, so one must use undistorted material. For this reason, sampling was limited almost exclusively to carbonates. Fossils in carbonates are generally not appreciably distorted, even though the rocks themselves may be compacted (Shinn *et al.* 1977). Some well preserved cranidia are used from non-carbonate rocks (e.g. some chert nodules), but the vast majority of specimens are from carbonates. (This lithologic restriction implies that the material represents an environmentally biased sample. However, the coarse scale of the analysis, as well as the fact that the patterns documented here are consistent with other work involving a broader range of environments (see below), suggest that this bias is unlikely to be the cause of the observed patterns.)

Sampling

Historically there has been one group of systematists that worked primarily on Cambrian trilobites and another group on post-Cambrian forms (Whittington 1954; Fortey, pers. comm.). Thus, Cambrian and Ordovician genus concepts are unlikely to be comparable, and sampling simply from a list of genera might impart a bias. One possible solution to this problem is to sample strictly randomly. This introduces an unknown amount of error or bias reflecting collecting methods. The magnitude of this bias should decrease as the size of collections and the number of collectors increases. Therefore, material for this study was drawn from large museum collections, both stratigraphic and systematic (at the United States National Museum, the Museum of Comparative Zoology (Harvard University), and the Yale Peabody Museum). While museum collections are not strictly random subsets of all available fossils, they probably represent a more random sampling than would a list of genera or species.

Specimens were chosen randomly from museum collections by looking through every drawer known to contain trilobites and selecting every specimen that was sufficiently well preserved to allow morphometric description. The number of usable specimens in the combined collections of the three museums is in the hundreds to thousands.

Random sampling presents problems of its own. Groups of species tend to show right-skewed abundance-frequency distributions. That is, there are many species with a low abundance and a few species with a high abundance (e.g. Koch 1987). It is therefore likely that completely random sampling would force patterns to be dominated by a few abundant species. In order to circumvent this problem, sampling was arbitrarily limited to a maximum of three specimens per species per time horizon per locality. (To avoid cumbersome working, I will hereafter use the phrase 'per population' without implying the same meaning for 'population' that a neontologist uses.) In this way, some degree of intra-populational variability is quantified, but the overdominance of very abundant species is avoided. (Because data from many time planes are stratigraphically lumped to increase sample sizes (see below), it is possible for more than three specimens from a species to occur within the data of a single stratigraphic interval.) Each datum in this study represents a single cranidium selected as described above. Total sample size is 560, representing over 250 genera and over 400 species. A list of genera and species used in this study, and the Fourier coefficients for all specimens, were given by Foote (1989*a*).

Clearly some taxonomic bias remains with this method of sampling, since it implicitly assumes that species represent some real and consistent unit. If a 'true' species is finely split into many nominal species then more sampling is permitted from this species than from a species which is not oversplit in this way. Since it is possible (see above) that Cambrian species are more finely split than Ordovician species, one would expect the morphologic differences among related Cambrian species to be systematically less than among related Ordovician species. However, the data do not indicate this bias. It is shown below that the morphologic difference among specimens within higher taxa does not systematically increase through time. Thus, although the analysis cannot be said to be completely free of taxonomic bias, whatever bias may be inherent at the species level does not appear to have a great effect.

Stratigraphic division

The traditional stratigraphic division of the Cambrian into Lower Cambrian, Middle Cambrian, and Upper Cambrian (e.g. Lochman-Balk and Wilson 1958; Robison 1964) is adopted here (Table 1). A recent, comprehensive correlation of Ordovician formations of the United States (Ross *et al.* 1982) divides the Ordovician into the Ibexian, Whiterockian, Mohawkian, and Cincinnatian Series. Because of the large hiatus in the Whiterockian, sample size for this series is very low. It would be

TABLE 1. Stratigraphic division and sample sizes. Ages and durations in parentheses based on Sloan (in press). Others based on Sepkoski (1979) and Ross *et al.* (1982). Ages in millions of years before present, rounded to nearest million years. Durations in millions of years.

Interval	Age at base	Duration	Sample size
Silurian	435 (438)		
Ordovician 3	465 (454)	30 (16)	73
Ordovician 2	485 (477)	20 (23)	127
Ordovician 1	504 (504)	19 (27)	116
Upper Cambrian	518 (527)	14 (23)	125
Middle Cambrian	540 (554)	22 (27)	86
Lower Cambrian (trilobite-bearing)	562 (577)	22 (23)	33

useful to have a subdivision of the Ordovician that involved roughly comparable intervals of time and comparable sample sizes. I have therefore divided the Ordovician into three informal intervals, Ordovician 1, Ordovician 2, and Ordovician 3 (Table 1). (It is shown below that using the conventional division into Ibexian, Whiterockian, Mohawkian, and Cincinnatian Series does not alter the evolutionary patterns documented here.) Ordovician 1 is defined as that the interval from the base of the Ordovician approximately to Ross's Zone N, near the middle of the Whiterockian (*c.* middle of the Llanvirnian). (The placement of the boundary between Ordovician 1 and Ordovician 2 is somewhat arbitrary, since it lies within an interval that is barren with respect to data collected here. This barren interval reflects the major unconformity between the Sauk and Tippecanoe sequences (Sloss 1963). All the trilobites studied are either clearly from the lower part of the Whiterockian or the upper part, but not from the middle.) The top of Ordovician 2 coincides with the Blackriverian/Rocklandian boundary (*c.* middle of the Caradocian), and the top of Ordovician 3 coincides with the Ordovician/Silurian boundary.

The ages given in Table 1 are not known with certainty, and reflect the time scale given by Sepkoski (1979) for the Cambrian, and Ross *et al.* (1982) for the Ordovician. The apparently long duration of Ordovician 3 may appear to present problems, but it should be noted that most of the data for Ordovician 3 (63 out of 73 specimens) are pre-Cincinnatian and so lie within roughly the first half of Ordovician 3. An alternative chronology (dates in parentheses in Table 1) of the Cambrian and Ordovician (Sloan in press) yields interval durations that are rather different (and less variable) than those based on Sepkoski (1979) and Ross *et al.* (1982). (For the dates presented here, the Whiterockian is arbitrarily divided in half.) Because this study does not use absolute ages (e.g. to calculate evolutionary rates), the finer details of dating are of minor importance.

Classification of specimens into suprageneric taxa

The genealogies of trilobites are generally not sufficiently well known that all suprageneric taxa represent natural groupings (e.g. Bergström 1973; Fortey and Chatterton 1988). No claim is made here that every taxon used is a clade. However, it is reasonable to assume for the sake of discussion that higher taxa are rough approximations to monophyletic groups. Eldredge (1977, p. 320) expressed the opinion that 'many, if not most' superfamilies as defined in Harrington (1959) 'seem reasonably homogeneous', i.e. 'more or less monophyletic'. This seems more reasonable for some taxa (e.g. Trinucleacea) than others (e.g. Ptychopariacea) (Fortey and Chatterton 1988).

For the purposes of analysing variability within and among higher taxa of trilobites, the level of the superfamily is used. This taxonomic level generally allows reasonably large sample sizes, and in many cases superfamilies appear to represent morphotypes. The classification used is primarily that of the *Treatise*. Although this classification is by no means perfect, it is often presented as the closest thing to a consensus (e.g. Clarkson 1986). Modifications to the *Treatise* classification were based on later work by Fortey and Owens (1975) (Proetida), Lane and Thomas (1983) (Scutelluina), and Fortey and Chatterton (1988) (Asaphina). The families Lecanopygidae and Plethopeltidae were included in the Proetida. These forms had not been sufficiently studied by Fortey and Owens (1975) to determine their affinities, but they are linked with other proetids in the *Treatise*. Genera named after the publication of the *Treatise* were generally classified according to the author's taxonomic assignment. Where suprageneric classification is not given but an author expresses belief in a certain relationship, that relationship was used for suprageneric assignment.

In cases where no superfamilies are defined (e.g. Redlichiina), suborders are treated as if consisting of a single superfamily; thus, these suborders are treated as taxa of rank equivalent to that of superfamilies. Similarly, where no suborders are defined (e.g. Odontopleurida), the order is treated as if consisting of a single superfamily. Of the 560 specimens used, 303 (54·1 %) are assigned to established superfamilies, 99 (17·7 %) are assigned to suborders treated here as superfamilies, and 158 (28·2 %) are assigned to orders treated here as superfamilies. Sample sizes for the higher taxa range from 1–50 and are given in Foote (1989*a*). The known stratigraphic range for the higher taxa correlates well with the stratigraphic range represented in this study (Foote 1989*a*).

The higher taxa are analysed as groups irrespective of their position in the taxonomic hierarchy. For example, if the Proetida were best considered a suborder of the Ptychopariida, or the Remopleuridacea a superfamily within the Ptychopariina rather than within the Asaphina, this would have absolutely no bearing on the analysis. In addition, reassignment of specimens to different families, genera or species would leave the analysis unaffected as long as they remained within the same suprafamilial taxon. An analysis (not presented here) using the suborder, rather than the superfamily, as the fundamental higher taxonomic unit yielded results in agreement with those presented here.

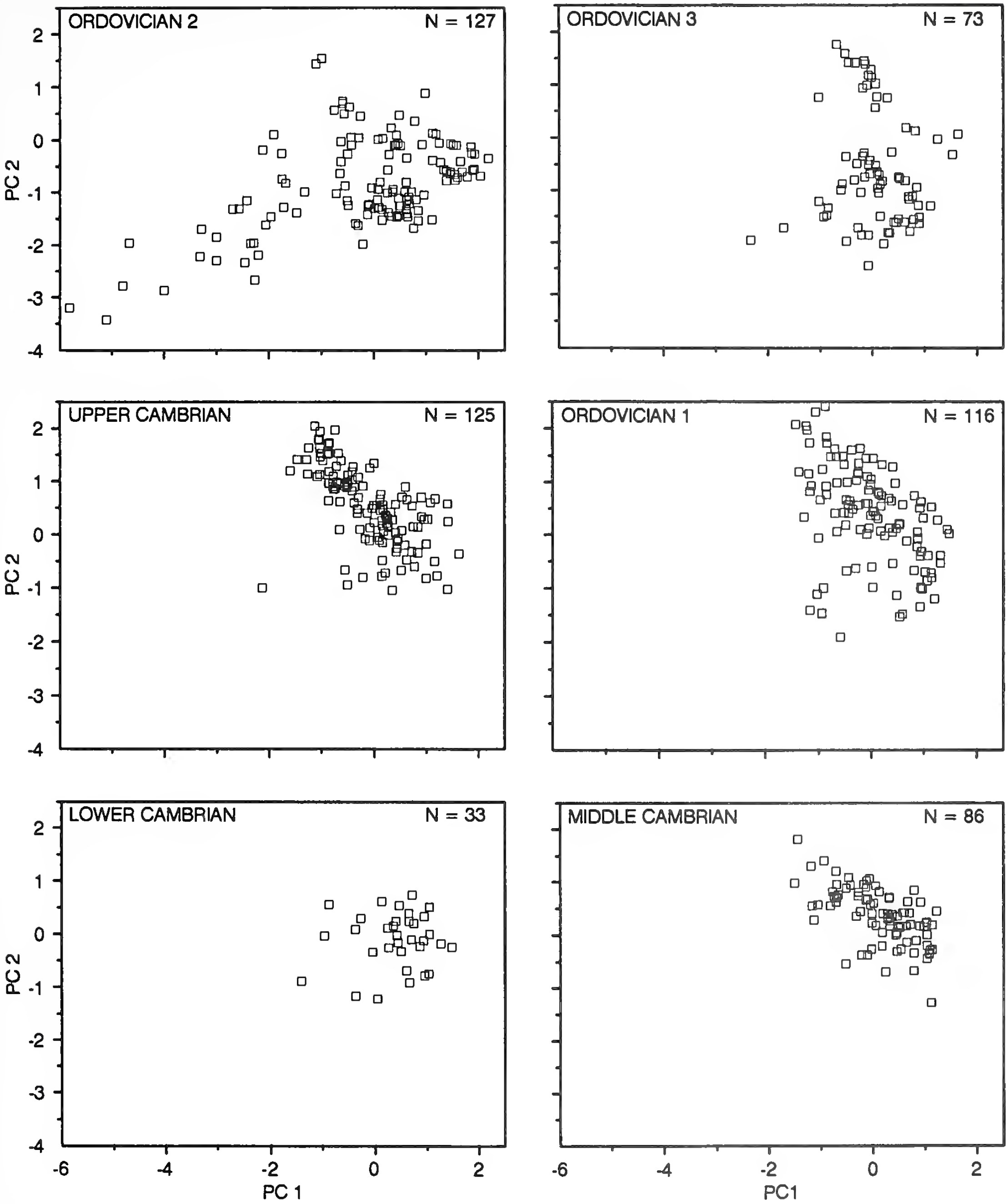
DATA ANALYSIS

Diversification within the Trilobita as a whole

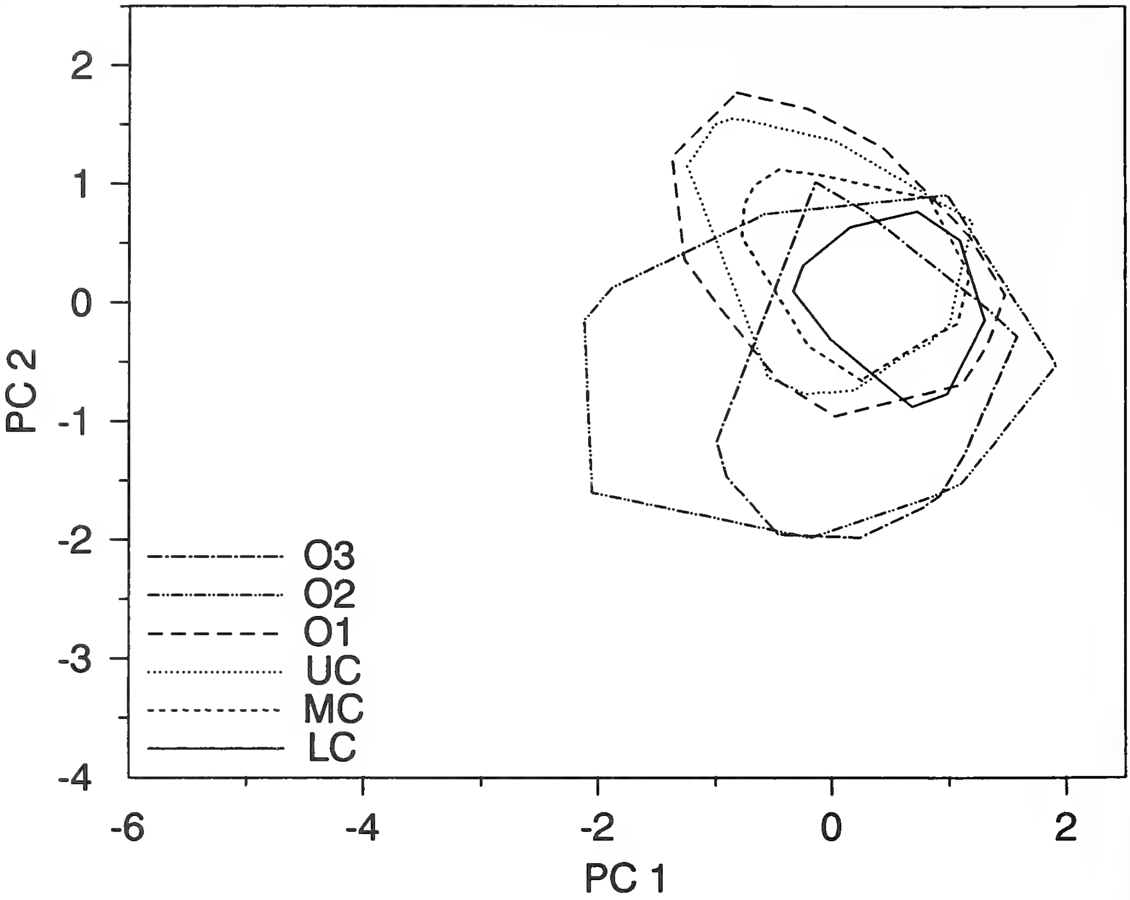
Before looking at the evolution of higher taxa of trilobites, it is useful to determine the patterns of morphologic diversity for the trilobites as a whole. Text-figure 1 shows all data plotted in a two-dimensional principal-component space, based on the correlation matrix of the original 12-dimensional morphospace of Fourier coefficients. (These two principal components summarize approximately 63 % of the variability among specimens contained in the 12-dimensional morphospace.) The principal components are used for graphical purposes only; later calculations are based on the complete, twelve-dimensional Fourier space. Inspection of Text-figure 1 reveals a clear increase in morphologic dispersion or variability through time.

Just a few morphologically extreme specimens could strongly affect one's visual impression of this pattern. It is therefore useful to remove the influence of extreme specimens. For each stratigraphic interval the morphologic centroid is determined. An envelope is then constructed which contains the 80 % of the data lying closest to the centroid (in the principal-component space) (Text-fig. 2). Thus, the most extreme 20 % of the data are excluded. Note that the figure 80 % is an arbitrary one, and this is not meant to be a robust statistical method for the removal of outliers. The point is to remove the effects of extreme forms without the assumption or belief that they 'don't belong'. It is clear from Text-figure 2 that the apparent increase in overall dispersion is not the result of a few extreme specimens.

That morphologic variability depicted in this way tends to increase is in agreement with what one would expect from a subjective assessment of the diversity of trilobite form. Comparing the diversity among post-Cambrian phacopids, asaphids, trinucleids, proetids, and odontopleurids to the diversity among Cambrian corynexochids, redlichiids and ptyhopariοids, the picture presented in Text-figures 1 and 2 should come as no surprise. Nevertheless, the quantitative documentation of this pattern is important and useful for at least two reasons. First, it allows a degree of confidence that is greater than that permitted by a subjective impression, no matter how keen. Second, it allows more detailed evolutionary questions to be addressed, such as the taxonomic level at which the diversification is concentrated (see below).



TEXT-FIG. 1. Trilobite cranidia plotted in principal-component space. Standardized scores for the first (PC 1) and second (PC 2) principal components are shown. Each point represents a single specimen. Sample sizes given by *N*.

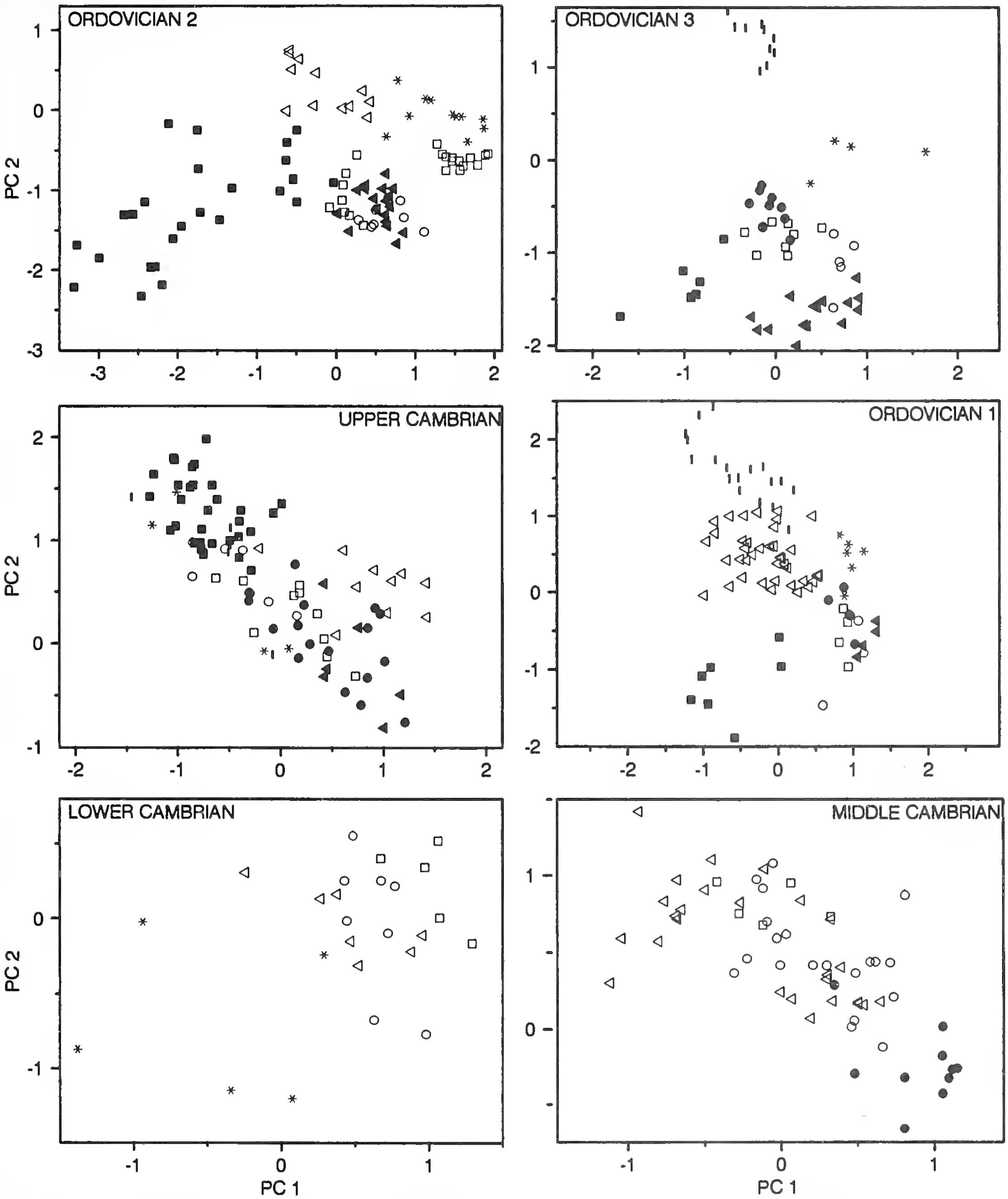


TEXT-FIG. 2. Envelopes surrounding the 80% of the specimens lying closest to the centroid for each respective stratigraphic interval. Axes as in Text-figure 1. Abbreviations: LC, Lower Cambrian; MC, Middle Cambrian; UC, Upper Cambrian; O1, Ordovician 1; O2, Ordovician 2; O3, Ordovician 3.

Even disregarding our knowledge of the fossil record of trilobites, such an increase in variability may be expected. As Stanley (1973) and Gould (1988) have argued, if a clade or lineage begins its history with a certain morphology, it is the null expectation that morphologic variance will increase as new and different forms evolve. It is intriguing that morphologic variability continues to increase into Ordovician 2, even though generic and familial diversity are greatest in the Middle to Upper Cambrian and decline through the Ordovician (Sepkoski 1982, 1984, and unpublished generic data). Even under conditions of decreasing taxonomic diversity, an increase in morphologic dispersion may be the null expectation if we consider morphologic evolution as a 'diffusive process'. The total range of morphospace occupied could tend to increase even if the number of biologic units occupying that morphospace decreased.

Preliminary analysis of higher taxa

The morphometric methods established above allow further questions to be addressed concerning the morphologic evolution of the trilobites. How does the gross pattern of diversification correlate with patterns among higher taxa? Does diversification proceed at many scales, and is the increase



TEXT-FIG. 3. Scatterplots of the 80% of the specimens for each group lying closest to the group centroid. Only groups with five or more specimens are shown. Axes as in Text-figure 1. Key: Lower Cambrian: △, Corynexochida; □, Eodiscina; ∗, Olenellina; ○, Ptychopariacea; Middle Cambrian: △, Corynexochida; □, Marjumiacea; ○, Ptychopariacea; ●, Solenopleuracea; Upper Cambrian: ■, Anomocaracea; ı, Illaenuracea; ▲, Komaspidacea; □, Marjumiacea; ∗, Raymondinacea; △, Proetida; ○, Ptychopariacea; ●, Solenopleuracea; Ordovician 1: ı, Asaphacea; ■, Cheirurina; □, Conocoryphacea; ∗, Cyclopygacea; ▲, Komaspidacea; ●, Olenacea; △, Proetida; ○, Scutelluina; Ordovician 2: ■, Cheirurina; □, Odontopleurida; △, Proetida; ∗, Remopleuridacea; ○, Scutelluina; ▲, Trinucleacea; Ordovician 3: ı, Asaphacea; other symbols as for Ordovician 2.

in dispersion evident within higher taxa as well? Do higher taxa represent morphotypes, as was implicitly assumed above?

The dispersion within and among higher taxa is depicted graphically in Text-figure 3. Here, only the 80% of the specimens lying closest to the morphologic centroid (in principal-component space) for each group are presented. As above, the purpose of this culling procedure is to remove the visual effect of extreme specimens. To keep the graphs simple, only groups with sample sizes of at least five are plotted. Two patterns are evident here:

1. There is no obvious tendency for within-group dispersion to increase through time. (Note that the scatterplots for different intervals are drawn at different scales.) At all times there are groups encompassing a large range of morphology, as well as morphologically more restricted taxa. This is true even though some of the higher taxa are at the level of the order.
2. The separation among groups clearly increases through time. This pattern is most striking when the Cambrian as a whole is compared to the Ordovician as a whole, but the trend is also evident within the Ordovician. Cambrian trilobites are difficult to partition into suprageneric groups that correspond to well-defined morphotypes, while at least some Ordovician taxa correspond to morphologically well defined units. This is in accord with previous observations (e.g. Rasetti 1954, 1961; Palmer 1958; Whittington 1966). It is likely that if more dimensions (i.e. morphologic variables) were added to this analysis, the Cambrian groups would become easier to discriminate. However, the fact that discrimination has historically been relatively difficult suggests that the difference between the Cambrian and the Ordovician is real.

Dispersion within groups shows no obvious trend, while dispersion among groups increases. This suggests that the overall morphologic diversification among the trilobites is tied to patterns at higher taxonomic levels. This is not meant to imply that there are superfamily-level evolutionary processes that differ fundamentally from evolutionary mechanisms within populations.

Quantitative analysis of higher taxa

The patterns depicted in two dimensions appear striking, but should be quantified in the 12-dimensional space. I emphasize that *all subsequent analyses in this paper are based on the complete, 12-dimensional Fourier space, not the principal-component space*. This quantification requires the use of multivariate measures of dispersion. There has been much discussion about how to measure morphologic dissimilarity (e.g. Van Valen 1974; Ashton and Rowell 1975; Atchley *et al.* 1982; Cherry *et al.* 1982). In principle, variances (e.g. Pearson 1926) and covariances (e.g. Atchley *et al.* 1982) should be taken into account when describing morphologic distances among groups. In practice, however, it has been found that simple distance measures that do not consider variances and covariances are more reliably estimated (Atchley *et al.* 1982; Cherry *et al.* 1982). Atchley *et al.* (1982) point out that simple distance measures may be more precise (i.e. more reliably estimated) but may be further from the morphologic 'truth'. For purposes of this study, it is more important that distance measures be reliable so that they can be compared among taxa and among times. Therefore, simple Euclidean distance is used here as a measure of morphologic dissimilarity. If there are p variables, then the Euclidean distance between two specimens is given by

$$d_{12} = \left[\sum_{j=1}^{p} (X_{j1} - X_{j2})^2 \right]^{\frac{1}{2}} \tag{1}$$

where X_{j1} and X_{j2} are the values of variable j on specimens 1 and 2.

Three dispersion indices were defined for the 12-dimensional Fourier space. W is the weighted mean of all within-group distances, and gives a measure of the morphologic variability within higher taxa. (Methods of weighting are discussed below.) A is the weighted mean of the distances among group centroids, and provides a measure of the morphologic variability among higher taxa. (The group centroid is an imaginary point representing the average morphology of the group, i.e., the arithmetic average for each of the variables measured on all specimens within a group.) Intuitively, it seems that the less dispersion there is within taxa and the greater the distance among taxa, the better defined or more distinct those taxa are. Therefore, discreteness, D, is defined as A/W. D is qualitatively similar to Mahalanobis' generalized distance, D^2 (Davis 1986, p. 486). D differs from Mahalanobis' D^2 in that it does not take into account variable correlations (which may not be reliably estimated for small sample sizes (Atchley *et al.* 1982; Cherry *et al.* 1982)), and does not assume a homogeneous variance–covariance structure.

In computing W, the number of pairwise comparisons increases with the square of the group sample size rather than with the sample size itself. This implies that large groups contribute disproportionately to the average distance. A method of weighting was used to correct for this. Within-group distances were weighted so that each group contributes to W according to its sample size rather than the number of comparisons made within that group. This method of weighting is explained below.

If: G is the number of groups; n_i is the number of specimens in group i ($i = 1, \ldots, G$); G' is the number of groups with $n_i > 1$ (i.e. the number of groups in which comparisons can be made); c_i is the number of pairwise comparisons in group i (equal to $n_i(n_i - 1)/2$; N is the total number specimens; N' is the total number of specimens in groups with $n_i > 1$ (i.e. the total number of specimens in groups in which comparisons can be made); d_{ijk} is the Euclidean distance between specimens j and k in group i; and $\bar{d}_i$ is the mean of all pairwise distances within group i, (equal to $\sum_{j=1}^{n_i} \sum_{k=j+1}^{n_i} d_{ijk}/c_i$); then W is defined as follows:

$$W = \frac{1}{N'} \sum_{i=1}^{G} \bar{d}_i n_i \tag{2}$$

where the sum is only over those groups where $n_i > 1$.

If A were computed without weighting, then a group with a large sample size, i.e. a group whose centroid is very reliably determined, and a group with a small sample size, i.e. a group whose centroid is less reliably determined, would make the same contribution to the average distance among groups (and therefore to the determination of discreteness, D). A method of weighting was used so that each group contributes to A in proportion to its sample size. Thus, groups whose position in morphospace is better determined have greater weight. This is explained below.

If: N, G, and n_i are defined as above; $\bar{n}$ is the average group sample size (equal to N/G); M is the number of comparisons among groups (equal to $G(G-1)/2$); and d_{ij} is the distance between the centroids of groups i *and* j; then

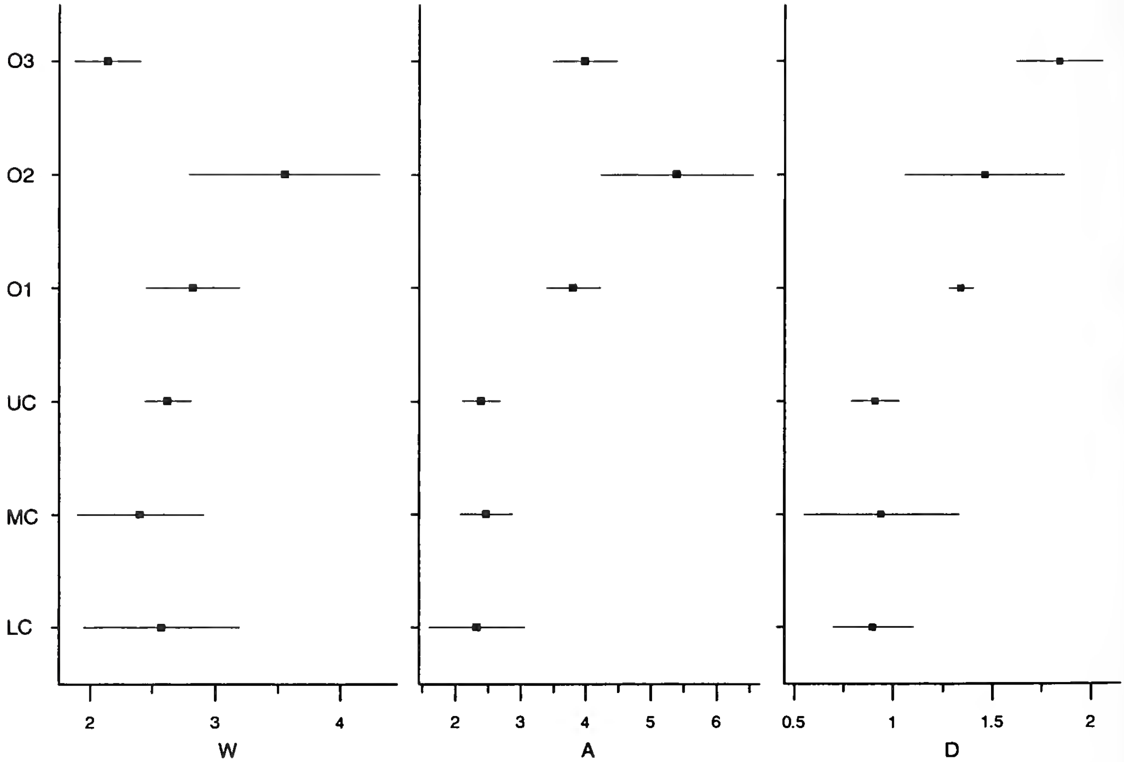
$$A = \frac{1}{2\bar{n}M} \sum_{i=1}^{G} \sum_{j=i+1}^{G} d_{ij}(n_i + n_j). \tag{3}$$

W, A, and D were computed for each of the six stratigraphic intervals. Two questions were addressed regarding temporal changes in dispersion indices. First, does the Cambrian as a whole differ from the Ordovician as a whole? This approach stresses the transition from the Cambrian to the Ordovician. Second, is there a monotonic trend in the dispersion indices? This approach stresses the continuity of the patterns. Some means of comparing these dispersion indices among the intervals is needed. This involves the estimation of how well constrained the indices are, i.e. the estimation of the standard error.

Jackknifing (Sokal and Rohlf 1981, p. 795) was used to obtain unbiased estimates of W, A, and D and to determine the variability associated with these estimates. By this method one group is omitted and W, A and D are recomputed. (Because W is not defined for a group with a sample size of one, it is recomputed only if the group omitted has a sample size greater than one.) If G_i is the number of groups in the ith interval, then a pseudovalue, Y_j, is calculated as $Y_j = G_i(X) - (G_i - 1)(X'_j)$, where X is the original value (i.e. W, A, or D), and X'_j is the value calculated when the jth group is omitted. (When calculating pseudovalues corresponding to W, G'_i is substituted for G_i.) Each group is left out in turn, and the mean of all the Y_j provides an unbiased estimate of X. The standard error of the Y_j provides an unbiased estimate of the standard error of X.

TABLE 2. Dispersion indices and their standard errors. In this and all subsequent tables, *G* is the number of higher taxa relevant to the calculation of *A* and *D*, *G′* is the number of higher taxa relevant to the calculation of *W*, and SE stands for 'standard error'. Abbreviations: LCAM, Lower Cambrian; MCAM, Middle Cambrian; UCAM, Upper Cambrian; ORD1, Ordovician 1; ORD2, Ordovician 2; ORD3, Ordovician 3.

Interval	*G*	*G′*	*W*	SE	*A*	SE	*D*	SE
LCAM	6	4	2·57	0·62	2·33	0·72	0·90	0·20
MCAM	9	6	2·40	0·50	2·47	0·39	0·94	0·39
UCAM	14	10	2·62	0·18	2·39	0·28	0·91	0·12
ORD1	10	10	2·82	0·37	3·80	0·41	1·34	0·06
ORD2	10	9	3·55	0·76	5·39	1·16	1·46	0·40
ORD3	8	8	2·14	0·26	3·98	0·49	1·84	0·22



TEXT-FIG. 4. Unbiased estimates of within- and among-group dispersion plotted against stratigraphic position. Error bars give one standard error on either side of dispersion index. Abbreviations as in Text-figure 2.

The unbiased estimates of *W*, *A*, and *D* are given with their standard errors in Table 2 and are shown in Text-figure 4. A method of comparing values through time is needed. One could use parametric statistical approaches, for example, making multiple comparisons among the values, or using the standard errors for analysis of variance. Using the standard errors estimated with jackknifing is analogous to treating each pseudovalue as if it were a single observation. Non-parametric statistical approaches are developed below, but this same approach is used: each pseudovalue is treated as a single datum.

To test for differences between the Cambrian and the Ordovician, the Kruskal–Wallis statistic, H (a non-parametric analogue to analysis of variance), was computed (Sokal and Rohlf 1981, p. 430). This method treats each observation (pseudovalue) as a ranked variate. For example, there are 57 observations (pseudovalues) computed for the analysis of A. In a ranking from lowest to highest, the six observations for the Lower Cambrian have ranks of 30, 2, 1, 14, 47, and 41, corresponding to the pseudovalues calculated when the groups Eodiscina, Corynexochida, Ptychopariacea, Solenopleuracea, Olenellina, and Redlichiina, respectively, are omitted. In the statistical testing of H, the distribution of ranks among categories (i.e. stratigraphic intervals) is compared to the distribution expected for a random partitioning of ranks. H is distributed approximately as χ^2 for a random partitioning (Sokal and Rohlf 1981, p. 432).

To test for monotonic changes in the dispersion indices, Kendall's rank correlation coefficient, τ, was computed (Sokal and Rohlf 1981, p. 602). The observations are ranked as above, and each stratigraphic interval is ranked from lowest to highest. Statistical tables were constructed by randomization. For example, in the testing of A there are six intervals with 6, 9, 14, 10, 10, and 8 groups, respectively. Thus the total number of observations is 57. The ranks 1 to 57 are randomly assigned to the six intervals with the constraint that the number of ranks assigned to each interval be equal to the actual number of observations in that interval. τ is then computed for the randomized ranks. This procedure is repeated 1000 times to construct a distribution of values of τ that would be expected by chance (Table 3). If an observed value of τ exceeds, say, 95% of the values obtained by randomization, this observed value is considered significant at $p = 0{\cdot}05$ and a monotonic trend is inferred. For the data studied here and for the culled data sets discussed below, distributions of τ were constructed and compared to the normal approximation (Burr 1960; Sokal and Rohlf 1981, p. 606; Rohlf and Sokal 1981, p. 77) (Table 3). Inspection of the results reveals that the distributions constructed by randomization are generally conservative for statistical testing, i.e., the null hypothesis of lack of monotonicity is less likely to be rejected.

TABLE 3. Critical values of τ, the rank correlation coefficient, generated by randomization. 'Tables' refers to other tables in the text to which these values are relevant. 'Indices' refers to dispersion indices in the relevant tables for which these values are used. Subscripts for τ refer to the significance levels generated by randomization. P-values give the corresponding significance level obtained using the normal approximation.

Tables	Indices	$\tau_{0\cdot05}$	P	$\tau_{0\cdot01}$	P	$\tau_{0\cdot001}$	P
4	W	0·215	0·033	0·272	0·0072	0·347	0·0006
4, 11	A, D	0·190	0·037	0·247	0·0068	0·285	0·00014
9	W, A, D	0·397	0·021	0·506	0·0034	0·599	0·0006
11	W	0·235	0·038	0·286	0·0062	0·323	0·002

As would be expected from the two-dimensional representations of higher taxa (Text-fig. 3), there is no significant change in within-group dispersion through time (Table 4). This result holds whether the Cambrian as a whole is compared to the Ordovician as a whole, or whether all six intervals are compared sequentially for monotonic changes. Thus, the obvious increase in total morphological dispersion among all trilobites does not result from the increase in the diversity of forms within an existing suprageneric taxon.

Also in agreement with the view presented in Text-figure 3, there is a significant increase in among-group dispersion (Table 4). The Cambrian as a whole differs from the Ordovician as a whole, and the changes among the six intervals indicate a monotonic trend. The total increase in dispersion among all trilobites is therefore linked to evolutionary patterns at taxonomic levels above that of the genus. This increase in among-group dispersion may result from either (1) the first appearance of new higher taxa that are morphologically well removed from their ancestors, or (2) the morphological divergence of established higher taxa, or some combination of these two. These

TABLE 4. Kruskal–Wallis statistics and Kendall rank correlation coefficients. In this and all subsequent tables, * indicates statistically significant at $P < 0{\cdot}05$, ** means significant at $P < 0{\cdot}01$, and *** means significant at $P < 0{\cdot}001$. All statistical tests in this study are two-sided.

Index	H	τ
W	0·600	0·029
A	14·676***	0·325***
D	14·191***	0·349***

alternatives are discussed below. Finally, given the significant increase in among-group dispersion and the lack of pattern in within-group dispersion, the morphologic discreteness of higher taxa increases through time (Table 4). This is in accord with previous observations that post-Cambrian trilobites are easier to classify into suprageneric taxa than are Cambrian forms (e.g. Whittington 1966).

Reality of morphotypes

In addition to investigating temporal changes in dispersion among taxa, it is important to determine whether, for a single stratigraphic interval, the taxa have some reality as morphotypes. One way to test this is to determine whether the discreteness value observed for a single stratigraphic interval differs significantly from discreteness values that would be expected for a random arrangement of specimens into groups. For each interval there are G groups with sample sizes n_i, $i = 1, \ldots, G$. Groups were artificially constructed so that the specimens were randomly divided among the G groups with the corresponding sample sizes. The discreteness, D, was then calculated for this random arrangement. One hundred unique randomizations were constructed for each stratigraphic interval, yielding a distribution of values of D that would be expected by chance. Comparison between observed values of D and the distributions of randomized values for each interval indicates that, with the possible exception of the Lower Cambrian, the arrangement of specimens into higher taxa is morphologically non-random (Table 5). Higher taxa of trilobites are thus shown to represent morphotypes, at least with respect to the shape of the cranidium.

TABLE 5. Number of randomized discreteness values greater than observed. Based on 100 randomizations.

Interval	N
Lower Cambrian	6
Middle Cambrian	0
Upper Cambrian	0
Ordovician 1	0
Ordovician 2	0
Ordovician 3	0

Analysis of persistent taxa

To determine whether new higher taxa are morphologically displaced from their ancestors, or established higher taxa move away from each other in morphospace, all higher taxa that appear in but a single interval were first removed from the data set, leaving all taxa that persist for two or more intervals. These remaining taxa were then arranged into sets of coexisting, persistent taxa to form smaller sets of data. Five such data sets were constructed and analysed as above (Tables 6–10). The rank correlation coefficient was computed only if the number of stratigraphic intervals was greater than two.

TABLE 6. Dispersion indices for Eodiscina, Corynexochida, Ptychopariacea and Solenopleuracea in Lower Cambrian and Middle Cambrian.

	Lower Cambrian	Middle Cambrian	*H*
G	4	4	
G′	3	4	
W (SE)	2·06 (0·28)	2·48 (0·55)	0·50
A (SE)	1·42 (0·62)	2·12 (0·66)	0·33
D (SE)	0·66 (0·34)	0·88 (0·32)	0·08

TABLE 7. Dispersion indices for Asaphiscacea, Crepicephalacea, Marjumiacea, Norwoodiacea, Ptychopariacea and Solenopleuracea in Middle Cambrian and Upper Cambrian.

	Middle Cambrian	Upper Cambrian	*H*
G	6	6	
G′	4	5	
W (SE)	1·89 (0·06)	2·62 (0·25)	4·86*
A (SE)	2·21 (0·59)	1·98 (0·41)	0·41
D (SE)	0·79 (0·36)	0·76 (0·17)	2·56

TABLE 8. Dispersion indices for Proetida, Komaspidacea, and Olenacea in Upper Cambrian and Ordovician 1.

	Upper Cambrian	Ordovician 1	*H*
G	3	3	
G′	2	3	
W (SE)	2·88 (0·39)	2·81 (0·52)	0·33
A (SE)	1·72 (0·08)	4·48 (1·56)	3·86*
D (SE)	0·56 (0·14)	1·75 (0·48)	3·86*

TABLE 9. Dispersion indices for Scutelluina, Cheirurina, Proetida, Asaphacea, Remopleuridacea and Trinucleacea in Ordovician 1, Ordovician 2, and Ordovician 3. *G′* is equal to *G* for all intervals. *H* measures the overall heterogeneity among the three intervals.

	ORD1	ORD2	ORD3	*H*	τ
G	6	6	6		
W (SE)	2·90 (0·63)	3·57 (1·13)	2·30 (0·32)	1·91	−0·27
A (SE)	3·90 (0·64)	4·81 (1·10)	4·46 (0·51)	0·22	0·21
D (SE)	1·33 (0·11)	1·26 (0·28)	1·92 (0·24)	3·94	0·428*

TABLE 10. Dispersion indices for Scutelluina, Odontopleurida, Cheirurina, Proetida, Asaphacea, Remopleuridacea and Trinucleacea in Ordovician 2 and Ordovician 3. *G′* is equal to *G* for both intervals.

	Ordovician 2	Ordovician 3	*H*
G	7	7	
W (SE)	3·48 (0·81)	2·30 (0·26)	1·80
A (SE)	4·38 (1·07)	4·13 (0·54)	0·20
D (SE)	1·25 (0·15)	1·78 (0·24)	2·55

If established higher taxa diverged morphologically, one would expect an increase in among-group dispersion within the subsets of persistent taxa. This is generally not the case. The only exception is the transition from the Upper Cambrian to Ordovician 1. Here a significant increase in among-group dispersion is marked by changes in taxonomic composition within the higher taxa. Komaspidacea in the Upper Cambrian is dominated by the Elviniidae, and in the Lower Ordovician by the Komaspididae. Perhaps more importantly, the Upper Cambrian Proetida are dominated by plethopeltids, and the Lower Ordovician Proetida by hystricurids. That higher taxa tend to occupy a relatively fixed place in morphospace is also evident from inspection of Text-figure 3.

Discussion

Since persistent higher taxa do not diverge appreciably, the significant increase in among-group dispersion is tied to the origin of new higher taxa. This might be seen as an inevitable consequence of the practice of classification. When forms show significant morphological divergence, they are perforce assigned to new higher taxa, leaving a paraphyletic residue. The phylogenetic relationships among higher taxa of trilobites are not sufficiently well known to state with certainty which groups are paraphyletic. However, the following discussion of higher taxa used in this study suggests that, at the least, we can be confident that paraphyly is more prevalent among Cambrian taxa than among post-Cambrian taxa.

Either Redlichiina or Olenellina would appear to be paraphyletic. If opisthoparian sutures are primitive, then Redlichiina may be seen as the paraphyletic ancestor of Olenellina (Eldredge 1977). If, on the other hand, lack of dorsal sutures is the primitive condition, then Olenellina may be the paraphyletic ancestor of Redlichiina (Fortey and Whittington 1989). Eodiscoids are probably derived relative to polymeroid trilobites, and primitive relative to agnostoids (Eldredge 1977; Fortey and Whittington 1989). This suggests that Eodiscina is the paraphyletic ancestor to holophyletic Agnostina. Lane and Thomas (1983), in expressing their belief in the relationship between Corynexochida and Scutelluina, left open the question of whether the corynexochids are a paraphyletic ancestor of Scutelluina, or a holophyletic sister group.

Paraphyly appears to be quite common among the ptychoparioid superfamilies. Robison (1987, p. 231) believes that 'many or most families [of trilobites] arose independently from an unspecialized stock (ptychoparian)...' As Eldredge (1977) points out, most similarities among trilobite groups represent symplesiomorphies, and many of the diagnoses of ptychoparioid superfamilies in the Treatise (Harrington *et al.* 1959) read like descriptions of a generalized trilobite. Of the superfamilies considered here, Asaphiscacea, Crepicephalacea, Komaspidacea, Leiostegiacea, Marjumiacea, Ptychopariacea, and Solenopleuracea seem to fit the description of a generalized ptychoparioid trilobite. On the other hand, a few ptychoparioid superfamilies are characterized by features that *may* be seen as valid synapomorphies. Conocoryphaceans lack eyes, norwoodiaceans are characterized by proparian or gonatoparian sutures, olenaceans have free cheeks that are fused or separated by a median suture, and raymondinaceans are characterized by cedariiform sutures (Harrington *et al.* 1959).

Phylogenetic analysis of the Asaphina (Fortey and Chatterton 1988) suggests that paraphyly is much less common in this predominantly post-Cambrian suborder. While Fortey and Chatterton believe the Asaphacea and Anomocaracea to be paraphyletic, Cyclopygacea, Dikelocephalacea, Remopleuridacea, and Trinucleaca appear to be holophyletic (Fortey and Chatterton 1988). Although not supported completely by formal phylogenetic analysis, it would seem that other post-Cambrian taxa are quite homogeneous and well derived, so that they are likely to be holophyletic. These include Harpina, Lichida, Odontopleurida, Phacopina, Proetida, and Scutelluina.

While the greater prevalence of paraphyletic taxa in the Cambrian no doubt contributes to patterns of within- and among-group dispersion, one observation suggests that this bias is not alone responsible. If taxonomic practice forced among-group dispersion to increase in the way outlined above, it could be argued that the increase should be rather regular. Instead, there is a large jump from the Upper Cambrian to Ordovician 1, and even within the Ordovician the increase can be seen. But within the Cambrian there is virtually no change in among-group dispersion. There is something about the distribution of forms in the Ordovician that *allows* systematists to define groups in such a way that newer groups are morphologically far removed and distinct relative to older taxa. If the separation of younger taxa were merely the result of this taxonomic artifact, then one would expect to see the pattern within the Cambrian, *if the distribution of Cambrian forms allowed this taxonomic practice to be exercised.*

Taxonomic artifact of another sort must also be considered. As discussed above and elsewhere (e.g. Whittington 1954; Foote 1988), it is possible that Cambrian and post-Cambrian genus concepts are not wholly compatible. The sampling methods employed here were designed to circumvent this bias. However, if taxonomic concepts were disparate at higher levels as well, this difference could, in part, cause the patterns seen here. The results shown above could conceivably tell more about changes in taxonomic practice than in the occupation of morphospace. However, changes in taxonomic practice are not independent of changes in the distribution of forms. It seems reasonable to suppose that if genera in the Cambrian showed a distribution of forms that would allow them to be arranged into discrete suprageneric taxa, then they would have been. Simply put, the results of this quantitative analysis are in agreement with what students of trilobites have long known regarding the distinctness of higher taxa (e.g. Rasetti 1954, 1961; Whittington 1954, 1966; Palmer 1958).

The pattern of increasing taxonomic separation is clearly linked to the overall morphological diversification of the trilobites. It is conceivable that Cambrian forms are difficult to arrange into discrete suprageneric groups because the total amount of morphospace occupied is so small. It is also possible that taxonomic separation is high in the Ordovician because of the influence of a few extreme groups. Ordovician taxa in the inner regions of morphospace might be similar in distinctness to Cambrian taxa. If so, the increase in average separation could be caused by the large among-group distances associated with the morphologically peripheral taxa. However, the observed pattern is not the result of these two factors, as shown by the following analysis.

The morphologic centroid (in the complete, 12-dimensional space) was calculated for each stratigraphic interval. A morphologic distance was chosen that defines a hypersphere centred on the Middle Cambrian centroid, and within which 90% of the Middle Cambrian data happen to fall. (This choice is somewhat arbitrary, but is justifiable. A much smaller volume would exclude too much of the Ordovician data. For example, the volume containing 80% of the Middle Cambrian data includes only 14% of the data of Ordovician 2, and therefore makes statistical analysis dubious. On the other hand, a much larger volume would include too much data, and therefore make the analysis nearly identical with that presented above.) The same volume is placed in turn in each of the six stratigraphic intervals, centred on the morphologic centroid for that interval. This constant volume contains 79% of the Lower Cambrian data, 90% for the Middle Cambrian, 77% for the Upper Cambrian, 59% for Ordovician 1, 44% for Ordovician 2, and 58% for Ordovician 3.

Analyses of the data within the constant volume indicates the same pattern as the unculled data. There is no significant change in within-group dispersion, but among-group dispersion and discreteness increase significantly. This implies that the pattern is not caused by extreme taxa, and can be detected at a smaller scale. With respect to taxonomic practice, we can conclude that Cambrian forms are difficult to classify into discrete higher taxa not because the total amount of morphospace occupied is smaller, but because the Ordovician morphospace is occupied in a more discontinuous manner.

BIASES IN DATA COLLECTION AND STRATIGRAPHIC CLASSIFICATION

Several analyses are presented below to correct for various potential biases in data collection and stratigraphic classification. These analyses involve subsets of data that are culled from the original data set. Space limitations preclude detailed presentation of results, but all further analyses yield patterns in general agreement with those presented above. More detailed treatment can be found in Foote (1989*a*).

General statement regarding data standardization

As explained above, all data were standardized to allow for equal weighting of the variables. Because the standardized variates depend on the calculated mean and standard deviation of the original variates, they will differ somewhat depending on whether the data are standardized before or after culling. The following general guideline is used to decide when to perform the standardization. If the purpose of culling is to correct for a bias that is expected to 'distort' the morphospace, then standardization is done after culling. (For example, oversampling of a particular group or time period would bias the mean and standard deviation, so standardization would be done after the oversampled data were removed.) Otherwise, data would be standardized before culling.

Differences in sample size

It is conceivable that changes in sample size could contribute to the pattern in group separation. For example, an increase in sample size would increase the chance of sampling morphologically extreme forms, and this could tend to increase the apparent dispersion among groups. This seems unlikely *a priori*. The Upper Cambrian, Ordovician 1, and Ordovician 2 have roughly the same sample sizes, but the pattern of increasing among-group dispersion is still evident if these intervals are compared (Table 2). Nevertheless, the effects of this potential bias should be treated explicitly.

To do so, the data were culled in two ways: (1) The Lower Cambrian was omitted because of its very small sample size, and from each of the remaining five intervals 73 specimens (corresponding to the smallest of the sample sizes, that for Ordovician 3) were chosen at random. (2) The Lower Cambrian was retained, and 33 specimens (corresponding to the Lower Cambrian sample size) were randomly chosen from each interval. In both cases the data were standardized after culling and were subjected to the same analysis outlined above. The results of this analysis are in agreement with those presented above, indicating that differences in sample size are not the cause of the observed patterns.

Sampling procedure

Perhaps more significant than sample size itself is the way in which specimens were chosen. The sampling procedure described above allowed up to three specimens per population to be sampled. Systematic changes in abundance could bias the pattern of within-group variability. There are more species in the Ordovician that are represented well enough in museum collections to reach this 'saturation point' of three specimens per population. This partly reflects the diverse silicified faunas from the Ibexian of Utah (Ross 1951) and the Whiterockian and Mohawkian of Virginia (Whittington 1941, 1956, 1959; Whittington and Evitt 1953). In general, replicates of the same species reduce the amount of within-group dispersion, since replication results in more within-species comparisons, i.e. more small distances. If this bias were strong enough it would artificially

TABLE 11. Dispersion indices for data set allowing maximum of one specimen per population. Abbreviations for stratigraphic intervals as in Table 2.

	G	G'	W (SE)	A (SE)	D (SE)
LCAM	6	4	3·01 (0·72)	2·42 (0·75)	0·80 (0·17)
MCAM	9	6	2·42 (0·51)	2·48 (0·41)	0·94 (0·36)
UCAM	14	10	2·69 (0·19)	2·37 (0·27)	0·88 (0·11)
ORD1	10	9	3·06 (0·42)	3·87 (0·45)	1·26 (0·08)
ORD2	10	8	3·81 (0·82)	5·68 (1·2)	1·42 (0·43)
ORD3	8	7	2·27 (0·31)	4·12 (0·51)	1·79 (0·26)
H			0·98	17·49***	13·13***
τ			0·051	0·352**	0·353**

increase the apparent discreteness of the Ordovician groups. To eliminate this bias the data were culled so that a maximum of a single specimen per population was retained. The data were standardized after culling, and analysed as above.

As would be expected, within-group dispersion for all stratigraphic intervals is higher when the replicates are removed (Table 11). Although this effect appears to be greater in the Ordovician, it does not significantly alter the patterns observed. Of course, this does not address the issue of what would have happened had a different limit been imposed, say six replicates rather than three. But the small difference between one and three replicates suggests that the effect would probably have been small. It is likely that unlimited (i.e. completely random) sampling would have a greater effect, but such a method of sampling is difficult to justify, as explained above.

Extreme data

There are two types of extreme data that could potentially affect the evolutionary patterns observed: (1) specimens that are extreme relative to the majority of specimens within a stratigraphic interval, and (2) specimens within a group that lie at the morphological periphery of that group. A few extreme data of the first kind in the Ordovician could conceivably cause the observed increase in among-group distance, but this appears not to be the case here. This potential bias was implicitly tested above when the data were culled to exclude all specimens lying outside a certain constant volume in morphospace. The same patterns are seen near the centre of morphospace as throughout the entire morphospace.

Extreme specimens within a group may increase mean within-group distance. To determine whether such specimens have a strong effect, the data were culled as follows. The morphological centroids were determined for each group. The 80% of the specimens in each group falling closest to the group centroid were retained, and the remaining 20% of the data discarded. This procedure is not intended to define outliers statistically but rather to determine the effects of the morphologically least ordinary specimens within a group. It is not claimed that the specimens defined in this way as 'extreme' do not 'belong' in the data set, i.e., there is no 'distortion' of morphospace by these specimens. Therefore, the data were standardized before culling. The results indicate that none of the dispersion indices change as a result of culling in such a way as to alter the basic evolutionary pattern.

Small groups

There are several higher taxa that at certain times are represented by only a few specimens. Dispersion statistics for smaller groups are generally less reliable (Atchley *et al.* 1982). One way that small sample size is accounted for here is by using dispersion indices that do not rely on the estimation of the covariance structure of the variables. In addition, small groups are given less weight in the calculation of dispersion indices. Finally, as the analyses of culled data presented above indicate, the patterns observed are relatively robust in the face of changes in sample size. Nevertheless, it is worth testing explicitly for the effects that small group sizes might have on the determination of within- and among-group measures of dispersion.

To do so, the data were culled to remove all groups with less than an arbitrary minimum of five specimens. Because this culling procedure is intended to test whether small groups represent an unbiased subset of all groups rather than whether small groups 'distort' morphospace, the data were standardized before culling. Within- and among-group dispersion indices for the culled data are very similar to those for the unculled data. Furthermore, the pattern of secular changes in the dispersion indices is unaltered, suggesting that small groups do not bias the results. There is nothing intrinsically different about small groups relative to large groups with respect to morphologic dispersion.

Stratigraphic division of the Ordovician

Different aspects of sampling strategy and sample size appear to have but minor effects on the dispersion indices calculated here. It is possible, however, that the way in which the data are lumped has some influence. To test for this, an alternative method for subdividing the Ordovician was used, namely, the four-fold North American standard of Ibexian, Whiterockian, Mohawkian, and Cincinnatian series (Ross *et al.* 1982). Both the unculled data and the data culled to correct for sample size yield results in agreement with those obtained using the three-fold division of the Ordovician.

DISCUSSION

The analyses presented above indicate that the observed patterns of within- and among-group dispersion are unlikely to result from biases inherent in the methods of data collection and analysis. It should be noted that the different data sets that are analysed are not independent. Thus, the various results do not provide independent verification of the patterns.

How a morphospace is defined is one determinant of the patterns detected in that morphospace. This study has drawn conclusions about trilobite evolution based on the evolution of the trilobite cranidium. It might reasonably be asked what patterns would have emerged if a different aspect of trilobite form had been considered. Two facts suggest that the patterns would have been concordant with those documented here. First, the result that higher taxa in the Ordovician are more distinct than those in the Cambrian is in agreement with previous observations based on gross morphology (e.g. Whittington 1954, 1966). Many aspects of trilobite morphology have contributed to their classification (Harrington 1959). That patterns based on the cranidium agree with the general impressions of trilobite workers serves as an *a posteriori* justification for the choice of the cranidium in defining the trilobite morphospace. Second, Whittington (1988*a*, 1988*b*) has found that the hypostomes of post-Cambrian trilobites map well onto suprageneric groups, while Cambrian taxa are more difficult to characterize by their hypostomes. This provides independent documentation of the same pattern shown in this study, but with a completely different morphological system.

Interpretations of the results of this study are reliable only insofar as the taxa employed have biological reality. The classification of trilobites is certainly not at its acme. Future changes in classification will clearly affect the fine details and perhaps even the major features of the patterns presented. This study is not intended as the last word on the evolution of higher taxa of trilobites. But the approaches presented here are valid for the investigation of patterns in the occupation of trilobite morphospace.

Two potential biases in the analysis need to be considered, but cannot be dealt with by simple culling of the data. These are (1) variation in the duration of stratigraphic intervals, and (2) inaccuracies and inconsistencies in the definition of higher taxa.

Because of time-averaging, a greater variety of form is likely to be lumped within a stratigraphic interval in proportion to the amount of time represented by that interval. As more time is lumped into a single interval, the distinctness of higher taxa should decrease as time-averaging causes them to be represented by a more variable array of forms. Thus, a systematic decrease in the duration of intervals higher in the stratigraphic column could artificially induce an increase in discreteness. It appears, however, that this bias is not at work here. The dates for the boundaries of stratigraphic intervals cannot be taken too literally, but neither the conventional time scale nor that based on Sloan's work suggests a systematic shortening of interval lengths (Table 1). While there can be no doubt that the duration of an interval must affect the dispersion indices, secular changes in these indices are not the result of variations in interval length.

If there were changes in taxonomic turnover rates, then stratigraphic lumping could conceivably cause the patterns. Given intervals of equal duration, more variability would accumulate within a taxon (because of time-averaging) if turnover were more rapid. The rate of generic turnover in trilobites decreased from the Cambrian to the Ordovician (Foote 1988; Sloan in press), but Cambrian taxa apparently did not accumulate more morphologic variability within a stratigraphic interval. Within-group dispersion in the Cambrian is not significantly higher than in the Ordovician.

If there were inconsistencies in the concepts of higher taxa such as superfamilies, then these could conceivably bias the results of any analysis that relied on higher taxa as defined. It is argued above and elsewhere (e.g. Whittington 1954) that the apparent differences between Cambrian and

Ordovician taxa are unlikely to arise from different taxonomic practice alone. Nevertheless, it would be desirable to have greater compatibility among taxonomic concepts. One approach would be progressively to improve the taxonomy of trilobites. As higher categories are defined more consistently, different taxa at different times can be compared more meaningfully. And as higher taxa more closely approximate natural groups, evolutionary interpretations of patterns at the higher taxonomic level will be more reliable. Yet, there will always be room for improvement. Furthermore, the very existence of a taxonomy imposes structure on the analysis.

The finding that trilobite taxa become more distinct through time implies that the gaps in morphospace become more pronounced, and the clusters in morphospace tighter. As discussed above, each specimen is represented by a single point in morphospace. If the apparent pattern is not simply the result of taxonomic practice, then changes in the occupation of morphospace should be detected as changes in the degree of clustering of these points. Several methods exist in ecology (e.g. Clark and Evans 1954), physical cosmology (Peebles 1980), and other fields to quantify the intensity of clustering of points. Results based on a modification of one of these methods indicate that morphological clusters do become tighter from the Cambrian to the Ordovician. Therefore, the patterns documented here are not solely the result of taxonomic artifact (Foote 1989*a*).

Massive extinctions are potentially important in causing the patterns documented here. It is commonly argued that extinctions can foster subsequent radiations by clearing out large areas of ecospace (e.g. Valentine 1969; Colbert 1980, p. 443). While such radiations proceed by the multiplication of species, the scale and tempo of radiations into relatively empty ecospace result in patterns detected at higher taxonomic levels (Valentine 1969). The largest single increase in the separation among higher taxa of trilobites occurs in the transition from the Upper Cambrian to the Lower Ordovician. (Although the difference in among-group dispersion, A, between Ordovician 1 and Ordovician 2 is numerically slightly larger, the standard error associated with A in Ordovician 2 is so large as to make this transition less striking [Table 2].) The Upper Cambrian and Tremadocian both are well known as times of rapid turnover in the trilobites (e.g. Stubblefield 1960; Fortey 1983; Palmer 1984). Because of the importance of international correlation, much attention has been paid to the Cambro–Ordovician boundary itself (e.g. Bassett and Dean 1982). However, increased resolution (Sepkoski 1979, p. 223) and more detailed palaeontological investigation have shown that many Cambrian trilobite families endure into the Ordovician (e.g. Fortey 1983; Westrop and Ludvigsen 1987). Considering the coarse scale of analysis used here, the exact temporal distribution of the extinctions is not of the utmost importance. The extinctions were apparently sufficiently significant to effect the evacuation of ecospace, and play a role in the post-Cambrian radiation of higher taxa of trilobites (e.g. Stubblefield 1960).

The analyses presented above show that morphotypes become better defined and morphologic gaps become more pronounced through time. Within-group dispersion does not change significantly from the Cambrian to the Ordovician. The latter statement is somewhat misleading, however. Overall dispersion and the dispersion among higher taxa do increase substantially. Therefore, dispersion within groups decreases as a proportion of the total amount of morphospace occupied. There is a morphologic radiation, but diversification at lower levels does not keep up with diversification at higher levels.

Occupation of different adaptive zones by related groups of organisms is often marked by morphological differences among those groups (e.g. Van Valen 1971). The large divergence among trilobite morphotypes may indicate the colonization of new adaptive zones. Valentine (1969) saw the Palaeozoic radiation as taking place primarily by the subdivision of niches, while the Mesozoic and Cenozoic radiations involved the opening of new adaptive zones. The data here appear consistent with a slightly modified view of the Palaeozoic radiation (at least for trilobites). If morphotypes in some rough way can be said to approximate adaptive zones, then the morphologic radiation of trilobites in the middle and upper Cambrian, as Valentine (1969) said, may not proceed by the opening of new adaptive zones. But the Ordovician radiation of new morphotypes may indicate a change in the mode of diversification, involving the opening of new adaptive zones.

Higher taxa of trilobites represent discernible morphotypes, as shown by the non-random arrangement of specimens into higher taxa. However, these morphotypes need not represent adaptive zones. Raup and Gould (1974) showed that stochastic simulations of morphologic evolution result in clades that are morphologically distinct. Coherent morphotypes are to be expected from genealogical processes and may say nothing about adaptive themes. Similarly, an increase in the total range of morphospace occupied may be a null expectation (Raup and Gould 1974; Gould 1988).

How does the morphologic radiation of the trilobites compare to that in other groups? Campbell and Marshall (1987) analysed the diversification of the Echinodermata in terms of the origination of new characters. They concluded that the echinoderm classes do not converge morphologically toward their origin, but are distinct at their earliest occurrence. Smith (1988) has disputed this claim, arguing that it rests largely on taxonomic practice. Runnegar (1987) has expressed the opinion that early molluscan taxa are recognizable only in hindsight because they subsequently diversified. Yochelson (1979), however, believes that molluscan classes originated abruptly as morphologically distinct units. That different workers reach opposite conclusions working with the same material suggests that new approaches to the problem may be needed. In contrast to Campbell and Marshall's view of the Echinodermata and Yochelson's view of the Mollusca, the evidence from orders of mammals suggests that their Cenozoic radiation has largely involved continued morphological divergence (Simpson 1953, p. 226; Van Valen 1971).

As Campbell and Marshall (1987) imply, the issue underlying whether origins are 'sudden' is not just about differences in rates. It is also important whether morphologic divergence continues throughout the history of a group, or is concentrated in one or a few episodes. It cannot be argued that trilobite taxa are recognizable *merely* in hindsight, after they diverge and diversify. Quantitative, morphological evidence presented here demonstrates that higher taxa of trilobites, from the point in the stratigraphic record where they are recognizable as higher taxa, do not continue to diverge. In this respect, the origin of higher taxa of trilobites may justifiably be regarded as 'sudden'.

SUMMARY AND CONCLUSIONS

1. A Fourier description of the trilobite cranidium allows the quantitative documentation of morphologic diversification in the Cambrian and Ordovician.
2. Morphologic variability in the trilobites as a whole increased from the Early Cambrian to the Middle Ordovician, with a decline in the Late Ordovician.
3. Diversity of form and generic diversity do not correlate strongly. Previous work indicates that the latter showed a maximum in the Middle to Upper Cambrian, while results presented here show that the former was highest in the Middle Ordovician.
4. Morphologic dispersion within higher taxa of trilobites did not change significantly through time, although it did decrease in proportion to the total amount of morphospace occupied. This result is sensitive to the way higher taxa are defined.
5. Morphologic dispersion among higher taxa increased significantly from the Cambrian to the Ordovician, as did the morphologic distinctness of higher taxa. This pattern resulted from the origination of new higher taxa, not the divergence of established higher taxa. Patterns involving higher taxa are sensitive to the way that higher taxa are defined, but are not caused solely by taxonomic practice.
6. These patterns are observed even in confined regions in morphospace and therefore do not result solely from the contribution of extreme taxa.
7. The patterns do not result from any likely bias in data collection or treatment.
8. The cause for this increase in morphologic discontinuity is not clear. Possible explanations include (*a*) the expectation of a stochastic process and (*b*) radiation into new adaptive zones. The latter process was facilitated by extinctions in the Late Cambrian and Early Ordovician.

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THE *PALEORHINUS* BIOCHRON AND THE CORRELATION OF THE NON-MARINE UPPER TRIASSIC OF PANGAEA

by ADRIAN P. HUNT *and* SPENCER G. LUCAS

ABSTRACT. We describe a new skull of the phytosaur *Paleorhinus bransoni* from Palo Duro Canyon, Randall County, Texas. The genus *Paleorhinus* (synonyms, *Mesorhinus*, *Promystriosuchus*, *Francosuchus*, *Ebrachosuchus*, *Mesorhinosuchus*, *Parasuchus*) contains four valid species: *P. bransoni* (synonyms *P. parvus*, *P. scurriensis*), *P. neukami*, *P. magnoculus*, and *P. hislopi*. Other nominal species based on specimens that we assign to *Paleorhinus* are *nomina dubia*. *Paleorhinus* is a constituent of late Carnian faunas in the western United States (lower Dockum Group, Camp Springs Member of the Tecovas Formation, lower Chinle Formation, Popo Agie Formation), Germany (Blasensandstein), Morocco (Argana Formation), India (Maleri and Tiki Formations), and Austria (Opponitzer Beds). These faunas, together with correlative faunas which lack *Paleorhinus* in Scotland (Lossiemouth Sandstone Formation) and South America (upper Santa Maria and Ischigualasto Formations), encompass a *Paleorhinus* biochron which can be recognized across much of the Late Triassic of Pangaea. The age of this biochron is based on pollen, marine invertebrates, and radiometric dates.

PALO Duro Canyon in Randall County, Texas (Text-fig. 1) contains one of the most extensive exposures of the Tecovas and Trujillo Formations of the Upper Triassic. These strata have produced abundant vertebrate fossils elsewhere (e.g. Case 1922; Murry 1982, 1989; Chatterjee 1986), but relatively few from Palo Duro Canyon (Schaeffer and Gregory 1961; Schaeffer 1967; Long and Ballew 1985; Murry 1989). These collections include specimens of the phytosaur *Rutiodon* (Murry 1989), but no material of the generally older and more primitive phytosaur *Paleorhinus*. The nearest occurrence of *Paleorhinus* is about 200 km to the south at Home Creek, Crosby County (Case 1922). Here, we report a new occurrence of *Paleorhinus* in Palo Duro Canyon, which reveals a hitherto unknown faunal level in the Upper Triassic of this area. Phytosaurs are long-snouted, semi-amphibious vertebrates which constitute the majority of specimens collected in the Upper Triassic strata of western North America (Camp 1930; Gregory 1962).

The *Paleorhinus* skull from Palo Duro Canyon, Texas was discovered in 1966 by Nick Petruccione and David Hughes, and collection was supervised by Jack T. Hughes, Curator of Paleontology at the Panhandle Plains Museum. The locality is P217 in the locality records of the Panhandle Plains Museum (UTM 3,874,800 m N/ 256,850 m E Zone 14), and it lies just north of the northern boundary of Palo Duro Canyon State Park, on the west side of Palo Duro Creek in Randall County, Texas (Text-fig. 1). The skull was found in a basal conglomerate unit of the Upper Triassic strata, 0·25 m above the Permian Quartermaster Formation (Text-fig. 1), which also includes white sandstone and purple claystone. This conglomerate represents the northernmost outcrop of the Camp Springs Member of the Tecovas Formation, a stratigraphic unit that has yielded a skull of *Paleorhinus* in Scurry County, Texas (Langston 1949).

This article discusses the taxonomic status of the new skull, which necessitates a revision of the genus *Paleorhinus* and a consideration of all specimens assigned to this taxon. The widespread occurrence of this genus and its limited temporal range make it ideal for intercontinental correlation. The final portion of this paper discusses the definition and distribution of a *Paleorhinus* biochron throughout Pangaea.

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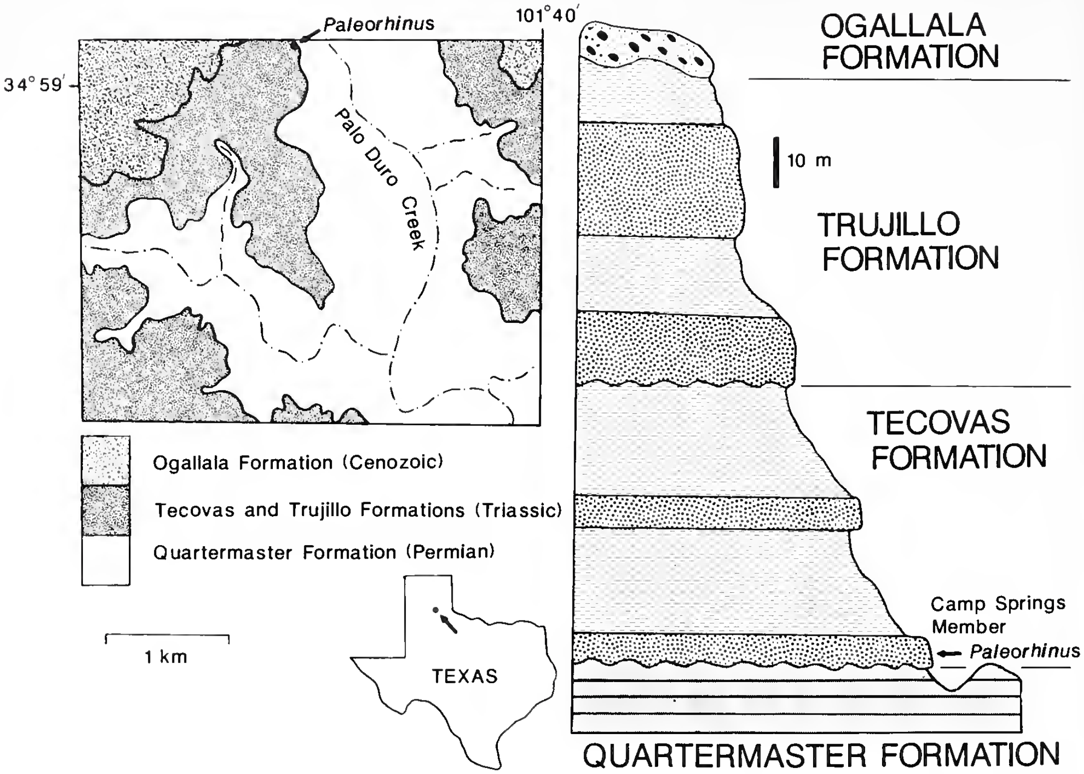


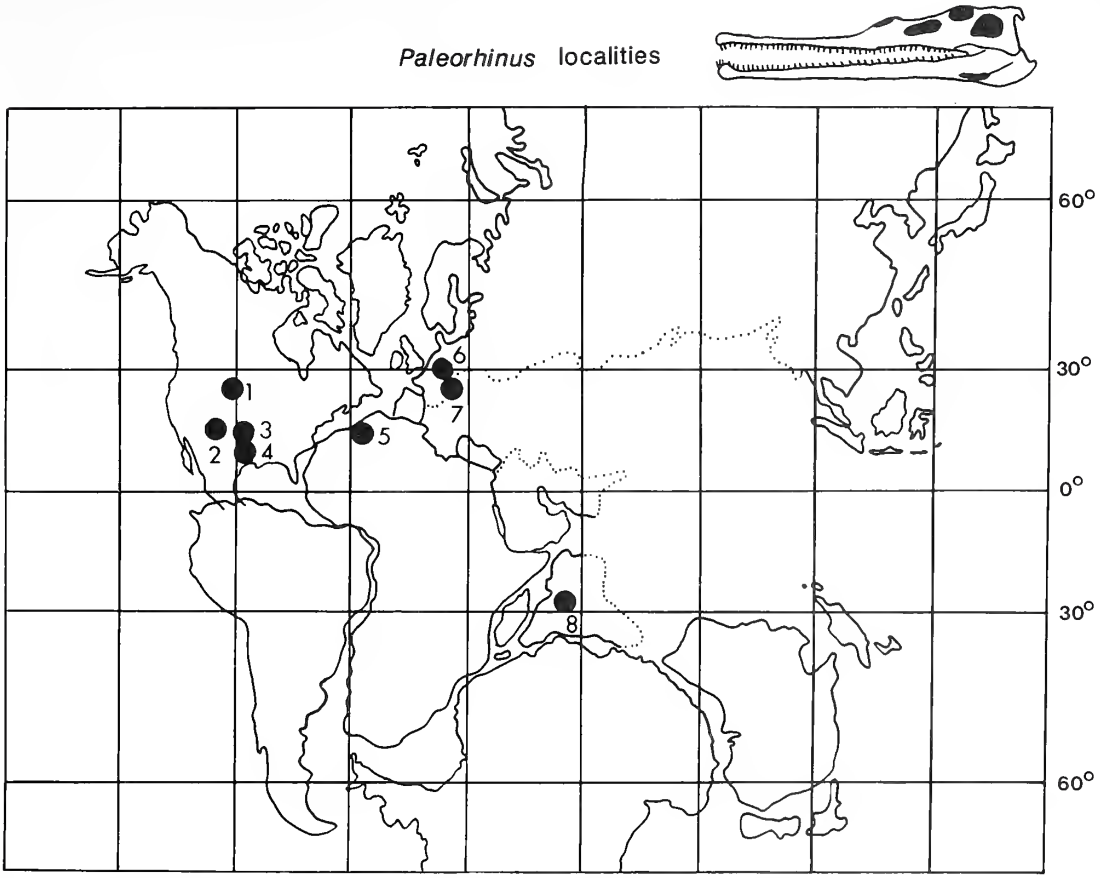
TEXT-FIG. 1. Geological map of part of Palo Duro Canyon, West Texas (after Matthews 1969), and a stratigraphic section showing the *Paleorhinus* locality.

Abbreviations. The following institutional abbreviations are used in this paper: FMNH UC, Field Museum of Natural History, University of Chicago Collection, Chicago, Illinois; MNA, Museum of Northern Arizona, Flagstaff, Arizona; MU, University of Missouri, Columbia, Missouri; NMMNH, New Mexico Museum of Natural History, Albuquerque, New Mexico; PPM, Panhandle Plains Museum, Canyon, Texas; TTUP, Texas Tech. University, Lubbock, Texas; UMMP, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; UT, University of Texas, Austin, Texas.

SYSTEMATIC PALAEONTOLOGY

Class REPTILIA Laurenti, 1768
Subclass DIAPSIDA Osborn, 1903
Order PSEUDOSUCHIA Zittel, 1890
Suborder PHYTOSAURIA Camp, 1930
Family PHYTOSAURIDAE Lydekker, 1888
PALEORHINUS Williston, 1904

1904 *Paleorhinus* Williston, p. 696, fig. 6.
1910 *Mesorhinus* Jaekel, p. 219, figs 2–6.
1922 *Promystriosuchus* Case, p. 49, fig. 21; Pl. 11A–D.
1932 *Francosuchus* Kuhn, p. 123, figs 5 and 6; Pl. 5, 1 and 2.
1936 *Ebrachosuchus* Kuhn, p. 77, fig. 4–5; Pl. 8, 1a–e; Pl. 10, 1 and 4.
1961 *Mesorhinosuchus* (*Mesorhinus*) Kuhn, p. 79.
1978 *Parasuchus* Chatterjee, p. 86, figs 1–14.



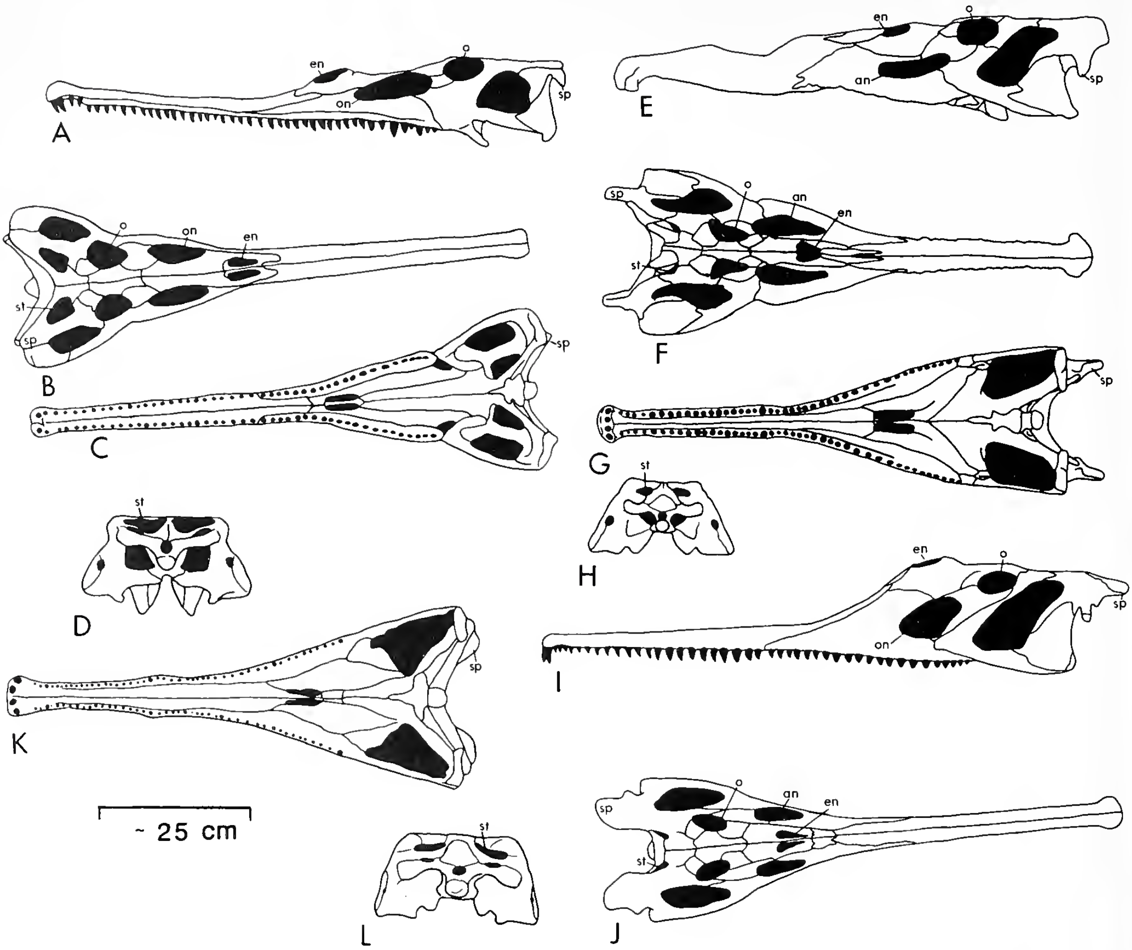
TEXT-FIG. 2. *Paleorhinus* localities of the Late Triassic Pangaean supercontinent. 1, Popo Agie Formation, central Wyoming (USA). 2, lowermost Petrified Forest Member of the Chinle Formation, northeastern Arizona (USA). 3, Camp Springs Member of the Tecovas Formation, Palo Duro Canyon, West Texas (USA; see Text-fig. 1). 4, lower part of undivided Dockum Group, Howard County, Texas (USA). 5, Argana Formation, Morocco. 6, Blasensandstein, West Germany. 7, Opponitzer Beds, Austria. 8, Maleri and Tiki Formation, India.

Type Species. Paleorhinus bransoni Williston, 1904.

Included species. The type species and *P. hislopi* Lydekker, 1885, *P. neukami* Kuhn, 1936, *P. magnoculus* Dutuit, 1977. The following named species are based on specimens of *Paleorhinus*, but are *nomina dubia*: *Mesorhinus fraasi* Jaekel, 1910, *Promystriosuchus ehlersi* Case, 1922, *Paleorhinus broilii* Kuhn, 1932, *Francosuchus latus* Kuhn, 1932, *Ebrachosuchus angustifrons* Kuhn, 1936, and cf. *Francosuchus trauthi* Huene, 1939.

Distribution. Popo Agie Formation of Wyoming, lower part of Petrified Forest Member of the Chinle Formation of Arizona, Camp Springs Member of the Tecovas Formation and lower part of Dockum Group (undivided) of West Texas, Blasensandstein (Germany), Opponitzer Beds (Austria), Argana Formation (Morocco), and Maleri and Tiki Formation (India) (Text-fig. 2). All these stratigraphic units are late Carnian (Late Triassic) in age (see later discussion).

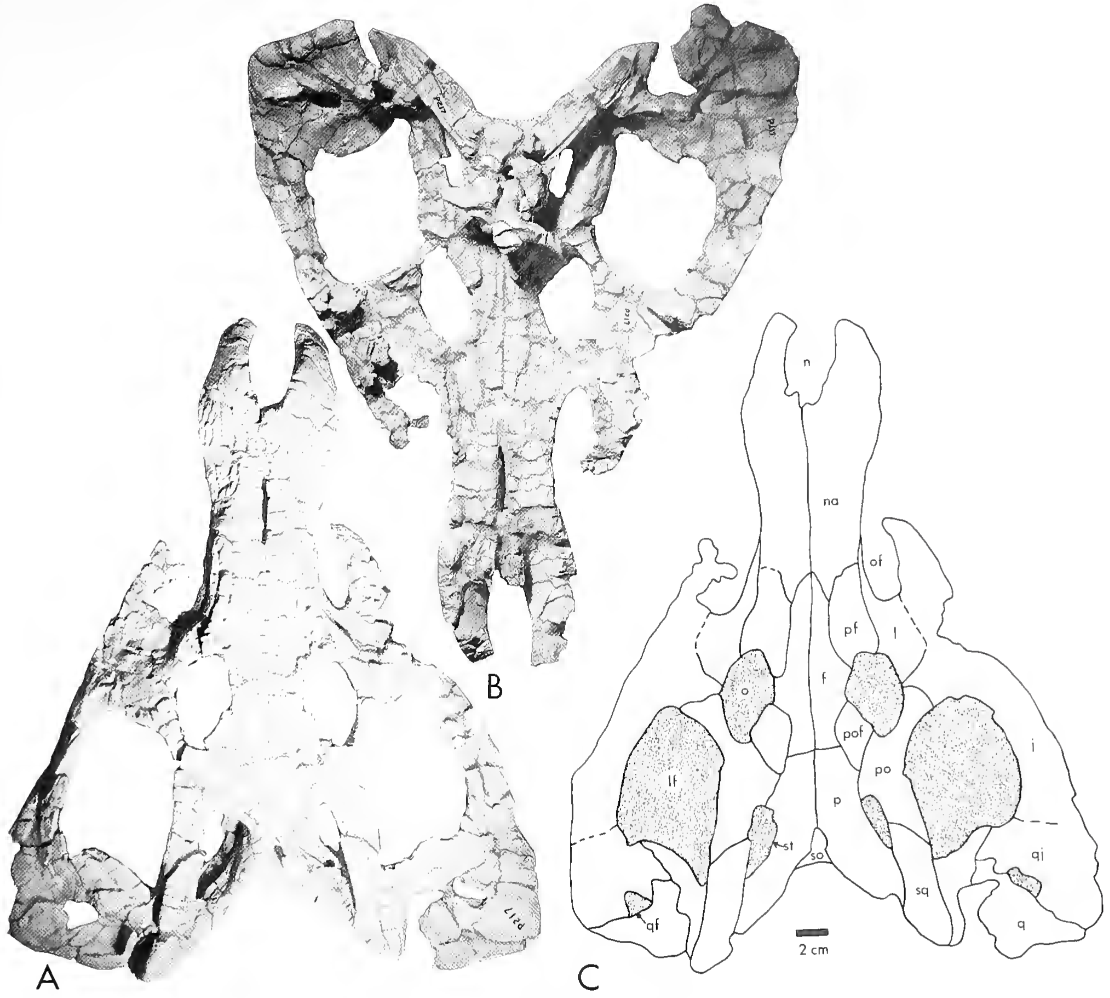
Revised Diagnosis. Phytosaurid that differs cranially from others in the following features: external nares lie anterior to the antorbital fenestrae; dorsal margin of external nares is inclined anteriorly; orbits are dorsally oriented; and quadratic foramina are large.



TEXT-FIG. 3. Skulls of the three common genera of Upper Triassic phytosaurs in North America, mid-late Carnian *Paleorhinus*, late Carnian *Rutiodon*, and Norian *Pseudopalatus*. A–D, *Paleorhinus* (after Chatterjee 1978); A, lateral view; B, dorsal view; C, ventral view; D, posterior view. E–H, *Rutiodon*; E, lateral view (after Case and White 1934); F, dorsal view (after Case and White 1934); G, ventral view (after Case 1922); H, posterior view (after Case 1922). I–L, *Pseudopalatus*; I, lateral view (after Camp 1930); J, dorsal view (after Mehl 1928*a*); K, ventral view (after Mehl 1922); L, posterior view (after Mehl 1928*a*). Abbreviations: an, antorbital fenestra; en, external nares; o, orbit; sp, squamosal process; and, st, supratemporal fenestra.

Discussion. *Paleorhinus* is the least derived phytosaur (Ballew 1989) because it has external nares anterior to the antorbital fenestrae and a posterior temporal arcade at the level of the skull roof (Text-fig. 3). The contemporary *Angistorhinus* also has a high posterior temporal arcade, but this genus has more posterior external nares. Phytosaurs of generally younger, Carnian age than *Paleorhinus*, such as *Rutiodon* (Text-fig. 3), are characterized by external nares above the antorbital fenestrae, posteriorly-rounded squamosal processes and a posterior temporal arcade that is wrapped around and under the posterior margin of the skull roof with small supratemporal fenestrae. Norian phytosaurs, such as *Pseudopalatus*, have slit-like supratemporal fenestrae and posteriorly-elongate squamosal processes (Text-fig. 3).

Several genera are here considered subjective junior synonyms of *Paleorhinus* (see above). Later discussion will indicate why we consider the type species of these genera to pertain to *Paleorhinus*.



TEXT-FIG. 4. *Paleorhinus bransoni*, PPM P217, incomplete skull from Palo Duro Canyon, West Texas. A, dorsal view. B, ventral view. C, drawing of dorsal view. Abbreviations: af, antorbital fenestra; f, frontal; j, jugal; l, lachrymal, lf, lateral fenestra; n, external nares; na, nasal; o, orbit; p, parietal; pf, prefrontal; po, postorbital; pof, postfrontal; q, quadrate; qf, quadratic foramen; so, supraoccipital; sq, squamosal; and, st, supratemporal fenestra.

Paleorhinus bransoni Williston, 1904

1904 *Paleorhinus bransoni* Williston, 1904, p. 696, fig. 6.
1928*b* *Paleorhinus parvus* Mehl, p. 142, figs 1 and 2; pl. 37, 1–10; pl. 38, 1–7; pl. 39, 1–2, 4.
1949 *Paleorhinus scurriensis* Langston, p. 325, figs 1–3.

Holotype. FMNH UC 632, skull (Williston 1904, fig. 6; Lees 1907, fig. 1–7).

Locality and Horizon. Popo Agie Formation (Upper Triassic) at Squaw Creek, southeast corner of Township 3 South, Range 1 East, Fremont County, Wyoming.

Referred specimen. PPM P217, a partial skull (Text-fig. 4).

Description of referred specimen. PPM P217 is a phytosaur skull that lacks the rostrum anterior to the external nares and portions of the maxillae lateral to them, and all palatal elements anterior to the posterior portion of the basisphenoid. The maximum length of the skull is 414 mm, with a maximum width of 357 mm, which has been increased by flattening of the skull. The skull is relatively undeformed, although the basioccipital has been pushed forward about 20 mm, and the ventral portions of the quadrates have been pushed posteriorly. The main deformation is the dorsoventral flattening evident in the orientation of the quadrates.

The external nares are well forward of the antorbital fenestrae, as is the case with '*Parasuchus*' *hislopi* (Chatterjee 1978), *Paleorhinus magnoculus* (Dutuit 1977) and *Paleorhinus bransoni* (Lees 1907). The antorbital fenestrae are relatively small. Although the anterior margins of both antorbital fenestrae are broken, the curvature of the upper and lower margins of the right fenestra indicates its original size. In dorsal view, the posterior margin of the skull appears very wide, but this is due to dorsoventral distortion. The external nares are inclined anteriorly. The lateral temporal fenestrae are roughly square in shape and have dorsal margins that are longer than the antorbital fenestrae. The quadratic foramina are large (19 mm maximum diameter) and visible in dorsal view because of the flattening of the skull. The sutural pattern is consistent with other specimens of *Paleorhinus* (e.g. Langston 1949; Chatterjee 1978).

PPM P217 is assigned to *Paleorhinus* on the basis of having external nares anterior to the antorbital fenestrae, external nares whose dorsal margins incline anteriorly, and the possession of large quadratic foramina. This specimen is assigned to *Paleorhinus bransoni* because of the small size of the orbits (cf. *P. magnoculus*) and inclusion of the jugal in the antorbital fenestrae (cf. '*Parasuchus*' *hislopi*: Chatterjee 1978, text-fig. 3*a*). The only morphological difference between *P. bransoni* and *P. neukami* is in the length of the rostrum, a feature not preserved in the new specimen. On the relatively weak grounds of geographic proximity, the new skull is thus identified as *Paleorhinus bransoni*.

PALEORHINUS TAXONOMY AND DISTRIBUTION

USA

Wyoming. Williston (1904) named *Paleorhinus* (type species *P. bransoni*) for a skull from the Popo Agie Formation at Squaw Creek in the Wind River Mountains of western Wyoming (Mehl 1928*b*). Williston (1904) briefly described the genoholotype of *P. bransoni*, and subsequently Lees (1907) described it in detail. Mehl (1915*b*, 1928*b*), Jaekel (1910) and Langston (1949) criticized several of Lees' (1907) interpretations of the structure of the *Paleorhinus* skull, but did not doubt its generic distinctiveness. Mehl (1915*a*, 1915*b*) demonstrated that an ilium assigned to *Paleorhinus* by Lees (1907) actually pertains to the rauisuchian *Poposaurus*.

Mehl (1928*b*) described a second partial skull and skeleton of *Paleorhinus* (MU 530), which he named *P. parvus*, from the Popo Agie Formation at Sage Creek in the same area of Wyoming as the type locality of *P. bransoni*. The skull and lower jaw of *Paleorhinus parvus*, which is now in three pieces, show no major differences from *P. bransoni*. Mehl (1928*b*, pp. 155–156) cited principally differences in the length of the rostrum and the degree of downward deflection of the rostral tip to distinguish *P. parvus*. However, he ignored the large size difference between the skulls of the two putative species. Colbert (1947) documented that relative rostral length is proportional to skull size in phytosaurs. In addition, the deflection of the rostral tip of the holotype skull of *P. parvus* is probably the result of post-burial deformation. Thus, we consider *P. parvus* a subjective junior synonym of *P. bransoni*.

Texas. Case (1922) named *Promystriosuchus ehlersi* for a badly fractured skull from the Tecovas Formation of Crosby County, Texas. Subsequently, Gregory (1962) included this taxon in *Paleorhinus*. '*Promystriosuchus*' differs from *Paleorhinus bransoni* in lacking a posterior squamosal hook in lateral view, but this could be the result of damage to the Texas skull. The holotype skull of *Promystriosuchus ehlersi* (UMMP V7487) is badly distorted and broken anteriorly along the midline so that, in ventral view, the right tooth row is directed ventrally, but the left tooth row is oriented laterally. Also, the lateral aspect of the left external naris is visible along the split midline of the skull. Gregory (1962, pp. 671–673) criticized Case's (1922) diagnosis of *Promystriosuchus ehlersi* in detail. We agree with Gregory (1962, pp. 672–673) that all the differences between

Paleorhinus bransoni and *Promystriosuchus ehlersi* cited by Case (1922) are either errors of interpretation or are characters now recognized as variable within phytosaur taxa. *P. ehlersi* apparently differs from *P. bransoni* in having a median narial septum which is not visible in lateral view. However, the holotype is so badly distorted and fractured that we consider *P. ehlersi* a *nomen dubium* at the species level, although its holotype clearly is a specimen of *Paleorhinus*.

Langston (1949) described *Paleorhinus scurriensis* from the Camp Springs Member of the Tecovas Formation at the base of the Dockum Group in Scurry County, Texas. The holotype (TTVP 539) is a partial skull that is similar to *P. bransoni* in having a more anterior placement of the nares than in *Promystriosuchus ehlersi*, but this is a variable feature within the genus *Paleorhinus* (Gregory 1962). Langston (1949, p. 325) used qualitative criteria to distinguish this species, including exceptionally large palatine foramina, moderately elongate posttemporal fenestrae, and dorso-ventral flattening of the skull. We do not consider these characters diagnostic, because the palate of most species of *Paleorhinus* is poorly known, fenestral shape is subject to postmortem deformation, and most *Paleorhinus* skulls are dorso-ventrally flattened. We are thus unable to diagnose *P. scurriensis* as a species separate from *P. bransoni*.

Six other undescribed skulls of *Paleorhinus* are known from Texas, one from the ?lower Tecovas of Borden County (UT 31213) and five from the lower Dockum Group of Howard County (UT 31100-453, 31100-101, 31100-239, 31100-418, 31025-172; Gregory 1962; Shelton 1984). Shelton (1984) referred all these specimens to *P. scurriensis*. However, as argued above, *P. scurriensis* and *Promystriosuchus ehlersi* are both conspecific with *P. bransoni*. Indeed, we have examined these specimens, and conclude that all the Texas *Paleorhinus* material represents one taxon, *P. bransoni*.

Arizona. A small fragment of a *Paleorhinus* skull (MNA V2698) has been collected from the Downs quarry in the lowermost levels of the Petrified Forest Member of the Chinle Formation in Apache County (Murry and Long 1989). This specimen has external nares anterior to the antorbital fenestrae, but cannot be identified beyond *Paleorhinus* sp.

New Mexico. Toepelman (1916, fig. 1) described a partial phytosaur rostrum from the Bluewater Creek Member of the Chinle Formation at Fort Wingate, McKinley County (Lucas and Hayden 1989) as ?*Paleorhinus*. However, this fragment is not diagnostic below the subordinal level (Hunt and Lucas 1989). Thus, there are no known occurrences of *Paleorhinus* in New Mexico.

Eastern USA. *Paleorhinus* has not been reported from the Newark Supergroup of eastern North America (USA and Canada). Historically, and recently, most phytosaur specimens from the Newark have been assigned to *Rutiodon*, regardless of how fragmentary the material is (e.g. Olsen 1989*a*, fig. 9.7). However, much of the Newark is Carnian in age, so it is possible that some of the fragmentary phytosaur material represents *Paleorhinus*. More complete specimens will be needed to evaluate this possibility.

Morocco

Dutuit (1977) described a nearly complete phytosaurid skull from the Argana Formation as *Paleorhinus magnoculus*. This species differs from other species of *Paleorhinus* in the enormous size of the orbits and, possibly, in the exclusion of the jugal from the antorbital fenestra.

India

Huxley (1870) used the name *Parasuchus* in a table, and this taxon was validated, and the species *P. hislopi* named, by Lydekker (1885) for fragmentary reptilian fossils from the Maleri Formation of the Pranhita–Godavari Valley. Subsequently, Huene (1940) identified one of these fragments as a basicranium of the rhynchosaur *Paradapedon*. The phytosaur specimens have since been referred to aff. *Brachysuchus maleriensis* by Huene (1940) and to *Phytosaurus maleriensis* by Colbert (1958). Gregory (1962) concluded that the type specimens of *Parasuchus hislopi* were generically indeterminate. Chatterjee (1974) designated a phytosaur rostral fragment from among the syntypes as the lectotype of *Parasuchus hislopi*, but this specimen is generically indeterminate, and thus the taxon is a *nomen dubium*. Virtually complete skeletons of a phytosaur have been collected from the Maleri Formation, and other specimens have been obtained from the Tiki Formation of the Son–Mahanadi Valley (Chatterjee 1967, 1978). Chatterjee (1978) referred these specimens to *Parasuchus*, but we follow Ballew (1989) in assigning them to *Paleorhinus*. Although the lectotype of *Parasuchus hislopi* may be a *nomen dubium*, we provisionally use the binominal *Paleorhinus hislopi* for all relevant specimens of '*Parasuchus*' pending a restudy of all the Indian specimens. The Indian species (*P. hislopi*) apparently differs from other species of *Paleorhinus* in lacking interpterygoid vacuities in the palate.

West Germany

Kuhn (1932, 1936) erected two genera and four species of phytosaurs from the Carnian Blasensandstein at Ebrach in Franconia. These taxa, *Francosuchus broilii*, *F. latus*, *Ebrachosuchus angustifrons* and *E. neukami*, are morphologically very similar to *Paleorhinus*. Indeed, Gregory (1962) and Westphal (1976) placed these taxa in a subgenus *Francosuchus* of the genus *Paleorhinus*. Chatterjee (1978) considered the specimens Kuhn described to represent the genus *Francosuchus*, which he placed in a different subfamily from *Paleorhinus*. However, the only major difference between the Ebrach specimens and other specimens of *Paleorhinus* is rostral length (Gregory 1962). *Francosuchus broilii* was originally reconstructed with a short snout (Kuhn 1932), but Kuhn (1936, p. 65) later realised that a portion of the snout was missing. The holotypes of *F. latus* (Kuhn 1932, fig. 5) and *E. angustifrons* both lack complete rostra, but that of *E. neukami* has a very elongate rostrum (Kuhn 1936, pl. 8, 1a–e). It is principally on the basis of the elongate rostrum of *E. neukami* that Gregory (1962) and Westphal (1976) placed all the Ebrach phytosaurs in a distinct subgenus from other *Paleorhinus* specimens. However, rostral length is a variable feature among phytosaurs (Gregory 1962), and we consider it a feature of taxonomic value only at the species level. Therefore, we do not uphold separate generic or subgeneric status for *Ebrachosuchus or Francosuchus*.

Chatterjee (1978) considered *Francosuchus* to be a separate genus on the basis of the position of the external nares relative to the antorbital fenestrae, which is a variable character (Gregory 1962), and the absence of posterior squamosal processes. However, the Ebrach skulls that have undamaged posterior margins exhibit posterior squamosal processes (Kuhn 1936, pl. 8, 1a; pl. 10, 5). Thus, we believe the taxonomic disposition of the Ebrach skulls should be to consider *Paleorhinus neukami* a distinct species based on its elongate rostrum, and to refer the other nominal taxa to *Paleorhinus* sp. because they lack diagnostic features.

Kuhn (1936) established another new phytosaur taxon from Ebrach, *Ebrachosaurus singularis*, that is obviously a *Stagonolepis*-like aetosaur, as noted by Benton and Walker (1985) (compare Kuhn 1936, pl. 13, 4 with Walker 1961, fig. 16, and Kuhn 1936, pl. 11, 1–3 with Walker 1961, fig. 20a–o). Kuhn also identified a lower jaw from Ebrach as *Mystriosuchus*, a Norian genus, but this specimen is indeterminate (Gregory 1962).

In 1910, Jaekel described a phytosaur skull, supposedly from the Buntsandstein (Lower Triassic) of Bernberg, as a new genus, *Mesorhinus*. There are several problems with this taxon. The holotype was found to have a label that read *Trematosaurus* (a labyrinthodont taxon: Jaekel 1910). The specimen is undoubtedly a phytosaur, but the label with the specimen indicated that it was from the Early Triassic, whereas all other phytosaur taxa are restricted to the Late Triassic (Jaekel 1910; Gregory 1962). Also, the holotype was destroyed in the Second World War (Gregory 1962). Jaekel (1910) attempted to verify the locality data on the label by examining the matrix around the specimen and concluded that it was, indeed, from the Buntsandstein, but this cannot now be checked.

Kuhn (1961) substituted the name *Mesorhinosuchus* for *Mesorhinus* because this name was preoccupied by that of a South American fossil mammal (Ameghino 1885). Recent authors have either considered *Mesorhinosuchus* Kuhn, 1961 (= *Mesorhinus* Jaekel, 1910) a tentative synonym of *Paleorhinus* (Gregory 1962; Westphal 1976) or as indeterminate (Chatterjee 1978). *Mesorhinosuchus* is undoubtedly a phytosaur (Walker 1968, p. 11; *contra* Gregory 1962, p. 675) of *Paleorhinus*-like morphology. It differs from all other adult phytosaurs in retaining a small pineal foramen (Jaekel 1910; Camp 1930), although the holotype of *P. scurriensis* has a shallow pit in this region (Langston 1949). *Mesorhinosuchus* is best considered as *Paleorhinus* sp. on the basis of the anterior placement of the nares. The age of the specimen must be considered indeterminate.

Austria

Huene (1939) coined the name cf. *Francosuchus trauthi* for a skull fragment of a phytosaur collected in 1905 near Lunz (about 110 km southwest of Vienna), Austria. This specimen was derived from dark gray to black shale of the lower part of the Opponitzer Schichten (Opponitzer Kalk of some authors) (Trauth 1948, p. 90). The Opponitzer Schichten of the Northern Alps are a predominantly marine-limestone unit of late Carnian (Tuvalian) age (Janoscheck and Matura 1980; H. Zapfe, written comm., 1989). The skull fragment Huene named cf. *Francosuchus trauthi* clearly pertains to *Paleorhinus* and thus establishes a link between the nonmarine occurrence of *Paleorhinus* and Triassic marine biochronology.

This skull fragment is number 1905/13 in the collection of the Naturhistorisches Museum of Vienna (a sharp resin cast is NMMNM P-12960) and was illustrated by Huene (1939, fig. 1a–c), Traúth (1948, fig. 14; pl. 12, figs 6 and 7) and Westphal (1976, fig. 7*e*). It is assignable to *Paleorhinus* because the external nares are obviously forward of the antorbital fenestae and lie on the posterior portion of the rostrum. This specimen, nevertheless, exhibits no other diagnostic characters and is here referred to *Paleorhinus* sp.

THE *PALEORHINUS* BIOCHRON

Cope (1875) first used fossil vertebrates to determine the age of red beds in the American West that we now recognize to be of Late Triassic age. Subsequently, Huene (1922*a*, 1922*b*, 1926) established a crude biochronology within these red beds, based principally on phytosaurs. Huene (1926, pp. 3, 4) noted that 'parasuchians such as *Palaeorhinus* [sic]..., having a supratemporal fenestra with a high posterior border, are relatively primitive and could not possibly be of Upper Triassic age' in contrast to phytosaurs from higher stratigraphic levels such as '?*Phytosaurus doughti*'' [sic] which he thought were of Late Triassic age.

Camp (1930), in the course of his revision of the phytosaurs, realized that Huene's two faunas were both of Late Triassic age and refined the biochronology to recognize four successive faunas. Camp (1930), like Huene (1926), realized that *Paleorhinus* is more primitive than other phytosaurs, although he failed to recognize that *Promystriosuchus* is congeneric with *Paleorhinus*.

Gregory (1962) published the next revision of the phytosaurs, and, in a series of articles (Gregory 1956, 1969; Colbert and Gregory 1957), he outlined a worldwide biochronology for the Late Triassic based on vertebrate faunas. Gregory (1956, 1969) recognized four faunas in North America, the oldest of which was defined by the co-occurrence of the phytosaurs *Paleorhinus* and *Angistorhinus*. Gregory (1956, 1969) correlated this fauna with the Blasensandstein of Germany. Chatterjee (1978) and Ballew (1989) subsequently used the occurrence of *Paleorhinus* to correlate the Argana Formation of Morocco and the Maleri and Tiki Formations of India with the Blasensandstein.

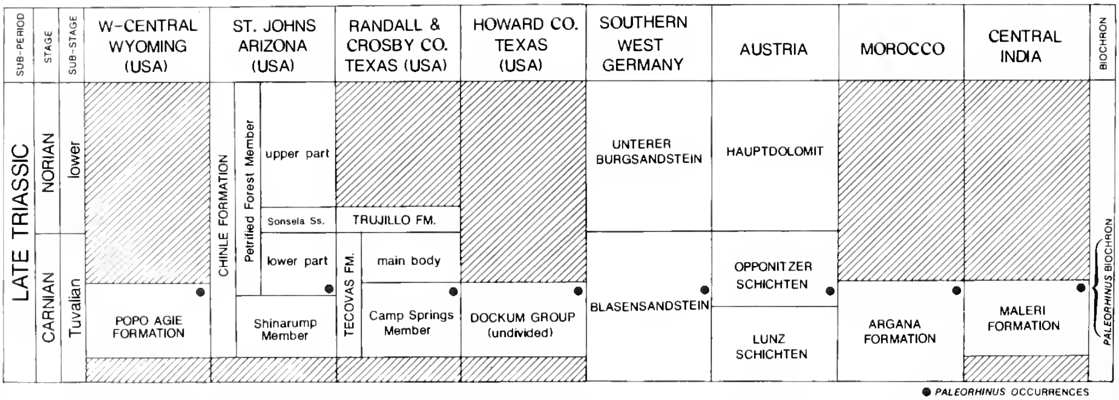
Paleorhinus occurs with faunas that are distinct from those of overlying or underlying strata and which vary geographically. The phytosaur *Angistorhinus* occurs in several faunas with *Paleorhinus* (Popo Agie, lower Dockum, Argana). The co-occurrence of the rhynchosaur *Hyperodapedon* with *Paleorhinus* in the Maleri Formation (Benton 1983) is strong evidence to suggest that the Lossiemouth Sandstone Formation of Scotland and the Wolfville Formation of Nova Scotia, which also contain *Hyperodapedon* (Benton 1983; Olsen 1989*b*), are also of the same age (*contra* Cooper 1982). A complicating factor is that the Lossiemouth fauna also includes the aetosaur *Stagonolepis* (Walker 1961; Benton and Walker 1985) which occurs in North America (*Calyptosuchus* of Long and Ballew 1985) with post-*Paleorhinus* phytosaurs (Murry and Long 1989).

The Ischigualasto Formation of Argentina and the upper Santa Maria Formation of Brazil contain the rhynchosaur *Scaphonyx* which is very similar to *Hyperodapedon* (Benton 1983) and are also probably of the same age. The Ischigualasto, Santa Maria, and Lossiemouth Sandstone Formations contain terrestrial faunas that lack semiaquatic taxa such as phytosaurs. Other tetrapod taxa that are found in *Paleorhinus*-bearing or equivalent faunas are aetosaurs (lower Dockum – *Longosuchus*; Blasensandstein – *Ebrachosuchus*; Maleri – undescribed; Ischigualasto/Santa Maria – *Aetosauroides*; Lossiemouth/lower Chinle – *Stagonolepis*), metoposaurs (Popo Agie, lower Dockum, Blasensandstein, Maleri, Argana), dicynodonts (Popo Agie, Argana, Ischigualasto), and rauisuchians (Popo Agie, lower Dockum, Maleri, Ischigualasto). Few of these taxa aid in correlation with the North American Late Triassic, but the rauisuchian *Poposaurus* occurs in the Popo Agie and the lower Dockum, and indistinguishable metoposaurs (Hunt 1989*a*) occur in the lower Dockum (*Buettneri howardensis*), Maleri (*Metoposaurus maleriensis*), Argana (*Metoposaurus azerouali*) and the Wolfville and Camp Springs (*Buettneria bakeri*: Case 1932; Baird 1986). In addition, the dicynodont *Moghreberia* from the Argana (Dutuit 1988) is very similar to *Placerias* from the lowermost Chinle (Camp and Welles 1956) and they may be congeneric (Lucas 1990). Thus, the aetosaurs, metoposaurs, dicynodonts and rauisuchians that occur in *Paleorhinus*-bearing strata or their equivalents are distinct from taxa in underlying and overlying strata.

In the western United States and Germany, *Paleorhinus*-bearing faunas are succeeded by faunas dominated by other phytosaur taxa. There are only two occurrences of overlap between *Paleorhinus* and more derived phytosaurs. At the Downs' quarry in the lower Petrified Forest Member of the Chinle Formation in northeastern Arizona, a single skull fragment of *Paleorhinus* (MNA V 2698) co-occurs with the phytosaur *Rutiodon*. The remainder of the Chinle phytosaur fauna is dominated by fossils of *Rutiodon* and *Pseudopalatus*. At Home Creek in Crosby County, Texas, Case (1922) reported the presence of *Paleorhinus* (= *Promystriosuchus*), but, subsequently, only specimens of *Rutiodon* have been found in this area (Gregory 1972). However, Case (1922) did not give exact geographic or stratigraphic information about his locality, and the *Paleorhinus*-bearing Camp Springs Member does crop out in this area (Finch and Wright 1983; Finch *et al.* 1976). Thus, the two taxa of phytosaurs may not co-occur in the same fauna in West Texas.

Paleorhinus occurs with faunas distinct from those of overlying and underlying strata that can be correlated throughout much of the world, and this taxon exhibits negligible stratigraphic overlap with other phytosaurs (Text-fig. 5). Therefore, we recognize a *Paleorhinus* biochron (Lucas and Hunt 1989) that has biochronological utility across Pangaea.

The faunas that contain *Paleorhinus* have been considered Carnian in age by all recent authors (Murry 1982, 1986, 1989; Lucas *et al.* 1985; Chatterjee 1986; Olsen and Sues 1986; Lucas and Hunt 1989; Ballew 1989). Data from palynology (lower Dockum, Blasensandstein), radiometric dating



TEXT-FIG. 5. Correlation of Upper Triassic *Paleorhinus*-bearing strata of Pangaea. See text for discussion.

(Ischigualasto) and marine invertebrates (Opponitzer Beds) have the potential of giving a more refined age for these faunas.

Paleorhinus sp. from the Opponitzer Beds from near Lunz in Austria was found associated with an upper Carnian brackish marine fauna (Huene 1939; Westphal 1976). This specimen thus can be correlated into the standard marine sequence of the Alpine province, via ammonites and pollen, that indicate it is of Tuvalian age (late Carnian: Janoscheck and Matura 1980). This ties the *Paleorhinus* biochron to Triassic marine biochronology.

The Ischigualasto Formation of the Ischigualasto–Ischichuca basin of northwestern Argentina is associated with basalt and diabases which yield radiometric ages with a mean of 224 ± 5 Ma (Gonzales and Toselli in Valencio *et al.* 1975). This date may be judged as approximately mid Carnian in age (Forster and Warrington 1985), but the spread of radiometric dates from the Ischigualasto is from early Carnian to early Norian (Forster and Warrington 1985).

The age relationships of strata of the Middle Keuper in Germany are somewhat controversial despite palynological studies (Benton 1986). The Blasensandstein, which contains *Paleorhinus*, is equivalent to part of the Rote Wand of southwestern Germany which has been considered earliest Norian or early late Carnian in age (Fisher 1972; Fisher and Bujak 1975; Kozur 1975; Gall *et al.*, 1977; Schroeder 1982). We prefer the latter correlation, as we believe that the unconformity at the base of the Stubensandstein may correlate with unconformities in other parts of the world that reflect a major eustatic fall of sea-level at the Carnian–Norian boundary (Embry 1988).

Dunay (1972) attempted to compare the palynology of the *Paleorhinus* and '*Phytosaurus*' (*Rutiodon*) zones of Gregory in the Tecovas Formation. However, Dunay's (1972) samples from the *Paleorhinus* zone were from Crosby County where, as he noted, *Rutiodon* is also found, and there are no good locality data for the older collections. Therefore, he may have sampled a *Paleorhinus* fauna, a *Rutiodon* fauna, or a transitional fauna that contains both (cf. Downs' quarry). However, Dunay (1972; Dunay and Fisher 1979) was certain that the palynofloras of the Tecovas Formation and the overlying Trujillo Formation were late Carnian in age. Litwin (1986) concluded that the lower Chinle Formation in Arizona that contains *Rutiodon*, a taxon characteristic of post-*Paleorhinus* strata in Texas, was also late Carnian in age. Palynological evidence thus suggests that the *Paleorhinus* biochron is of late-middle (middle Tuvalian), but not latest Carnian age.

Ash (1980) reviewed the biochronology of megafossil plants in North America and proposed a number of 'floral zones'. The only *Paleorhinus*-bearing stratigraphic unit that also contains megafossil plants is the Popo Agie Formation which Ash (1980) placed in his *Eoginkgoites* 'floral zone' of middle Carnian age. This age determination was based on palynological studies of the Newark Supergroup in Eastern North America (Cornet 1977) and vertebrate correlations. However, Ash (1980) only tentatively placed the Popo Agie flora in this zone, and the name-bearing taxon is only represented by ?*Eoginkgoites*. Thus, we have little confidence in assigning a middle Carnian age to the Popo Agie from the megafossil plants. Instead, we conclude that the Popo Agie is of late Carnian age.

Dutuit (1983) explained the cosmopolitan nature of Late Triassic faunas dominated by phytosaurs and metoposaurs as being due to marine dispersal by these animals. However, there is no evidence that these animals lived in marine conditions, and there are terrestrial rather than marine connections between most occurrences of these faunas (Buffetaut and Martin 1984). *Paleorhinus* was a cosmopolitan taxon in the late Carnian, but phytosaur taxa in the Norian are more restricted in their distribution (Ballew 1989). A similar situation is seen in metoposaurs (Hunt 1989*b*) and these changes reflect increased provincialization of faunas towards the end of the Late Triassic.

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